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Daily Growth Increments in Otoliths of Starry Flounder (*Platichthys stellatus*) and the Influence of Some Environmental Variables in Their Production

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CAMPANA, S. E., AND J. D. NEILSON. 1982. Daily growth increments in otoliths of starry flounder (*Platichthys stellatus*) and the influence of some environmental variables in their production. Can. J. Fish. Aquat. Sci. 39: 937–942.

Tetracycline injected into juvenile starry flounders (*Platichthys stellatus*) was incorporated into the periphery of the sagittal otoliths within 24 h. The resulting band, visible under ultraviolet light, was used as a dated mark on the otolith growth increments. This technique was used to verify that increments were laid down on a daily basis, both in field and laboratory environments. Subdaily increments were visible in otoliths of fishes reared under most environmental conditions. The production of daily increments in juvenile starry flounders preconditioned to a natural environmental regime was unaffected by photoperiod or temperature fluctuation, suggesting the presence of an internal circadian rhythm.

Key words: starry flounder, *Platichthys stellatus*; otoliths, daily rings, growth increments, circadian, tetracycline

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La tétracycline injectée à de jeunes plies du Pacifique (*Platichthys stellatus*) pénètre à la périphérie de la sagitta de l'otolithe en moins de 24 h. La bande qui en résulte et qui est visible à la lumière ultraviolette a servi de marque de date connue sur les zones de croissance de l'otolithe. Grâce à cette méthode, on a pu vérifier que les zones de croissance sont déposées sur base quotidienne, tant sur le terrain qu'en laboratoire. Chez des poissons élevés dans la plupart des milieux, on observe des zones de croissance presque quotidiennes. La production de zones de croissance quotidienne chez des plies du Pacifique acclimatées au préalable à un milieu naturel n'est pas influencée par la photopériode ou des variations de température, ce qui laisse supposer un rythme circadien.

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THE existence of daily growth increments on otoliths of marine and freshwater fishes has been both suggested (Schmidt and Fabrizio 1980; Steffensen 1980; Townsend 1980) and confirmed (Pannella 1971; Brothers et al. 1976; Struhsaker and Uchiyama 1976; Taubert and Coble 1977; Radtke 1978; Wild and Foreman 1980; Wilson and Larkin 1980). These concentrically formed increments have considerable potential for the exact determination of hatching dates and early life history growth rates of wild fish populations. However, daily increments are not always produced in some species (Wild and Foreman 1980) and at some ages (Pannella 1971), making the verification of the increment to age relationship essential before its application to the aging of wild populations.

Most daily increment verification studies to date have employed laboratory-reared fish of known hatching date. However, many species, including the starry flounder (*Platichthys stellatus*), are not easily reared from hatching in a laboratory environment. In addition, cyclical laboratory events may influence growth increment formation. As a result, laboratory results may not be applicable to wild populations. In a series of experiments, Taubert and Coble (1977) concluded that an internal biological clock entrained by a 24-h light–dark cycle was responsible for daily increment formation in young mouthbrooders. In contrast, Brothers (1978) regarded temperature fluctuation as the key factor to the timing of increment deposition in temperate stream fishes. Photoperiod and feeding were considered to be less significant as increment inducers. The possibility of an endogenous rhythmicity was not discussed.

Tetracycline application to a fish at a known date can be used in age validation studies (Holden and Vince 1973) and as a temporal mark in growth studies (Wild and Foreman 1980). Tetracycline is known to be incorporated into calcifying tissues in a fish during growth, depositing a band fluorescent under ultraviolet light (Weber and Ridgway 1967; Meunier and Boivin 1974). We used the tetracycline band as a temporal mark, first of all to verify the existence of daily growth increments in juvenile starry flounders, both in the laboratory and in situ, and secondly, to test the current suggestions on the role of possible environmental modifiers on the deposition of otolith daily growth increments.

Materials and Methods

Intraperitoneal injection of oxytetracycline hydrochloride (100 mg tetracycline/kg fish) resulted in deposition of a UV-fluorescent band on the sagittae of the flounders. Injected volume was 0.025 mL. Although similar results were achieved by immersing the fish in a 0.02% oxytetracycline/saline solution for 1 d, the experiments described herein were carried out by means of an injection. All experimental fish in this study were 4–8 cm in standard length and ~ 8 mo old.

To be effective as an accurately dated marker, the tetracycline must be incorporated into the otolith soon after application. To determine how quickly tetracycline was incorporated into the otolith, 12 flounders were injected and killed after 0, 6, 10, 24, and 48 h. Left- and right-hand-side sagittae were removed immediately and processed (see following paragraphs).

For the in situ experiment, 25 flounders were collected at the mouth of the Nooksak River in Bellingham Bay, Washington, on October 10, 1980. The fish were injected and placed immediately in a 3.1 × 3.1 × 1 m mesh enclosure in a tidal channel of the estuary. Five control fish were collected by seine and eight fish were sampled from the enclosure on October 24, 1980; further sampling was impossible because of flood waters. Unmarked control fish served to check for naturally occurring fluorescence not induced by tetracycline. Left and right sagittae were removed from the fish the same day, brushed clear of tissue, and attached sulcus-side down with instant glue onto a standard microscope slide. Slides were stored in darkness until processing. Dark storage for up to 4 mo resulted in no reduction of fluorescence intensity.

For the laboratory experiments, wild-collected flounders were first reared in the laboratory for 2 mo under a natural light–dark cycle. Five aquaria in separate, light-proof cubicles were stocked with 20 flounders each. Experimental conditions for each aquarium were designed to test the effect of photoperiod and temperature fluctuation upon increment deposition. Temperatures were selected to approximate those measured in situ. Twenty-four and 36-h photoperiods were tested at constant temperature, with the latter also tested in conjunction with a 36-h temperature cycle. Constant light conditions with a 36-h temperature cycle were used to examine the effect of temperature alone. If the periodicity of either variable is related to increment timing, the 36-h cycle should result in fish with 67% of the increments visible under a 24-h cycle. Fish were also exposed to constant conditions for each variable, in the event that fluctuation of either environmental variable entrained an endogenous circadian rhythm. All experimental conditions are detailed below:

1) photoperiod of 13 h light:11 h dark (i.e. a natural light regime); constant temperature at 15°C (= 13L:11D/CT).

2) 24 h light; constant temperature (= 24L/CT).

3) 24 h light; 24 h at 15°C:12 h at 18°C (= $24L/24T_1:12T_2$).

4) 24 h light:12 h dark; constant temperature (= 24L:12D/CT).

5) 24 h light:12 h dark; 24 h at 15°C:12 h at 18°C (= $24L:12D/24T_1:12T_2$).

Temperatures were monitored with a continuous temperature recorder accurate to 0.25°C. During temperature changes, the final temperature was reached less than 2 h after initiation. All lighting was fluorescent. One satiation feeding with live *Tubifex* and frozen zooplankton was given at a random time during a 24-h period, with some periods omitted totally to avoid any entrainment of daily growth patterns due to feeding periodicity. All fish were acclimated to experimental conditions for 2 wk prior to tetracycline injection. Five fish from each aquarium were sampled within 1 d of injection, with the remainder of the fish sampled 25–26 d and 43–47 d after injection.

Mounted sagittae were ground to a plane where the peripheral growth increments were most visible. Otolith slides were mounted on a grinding apparatus (Neilson and Geen 1981) coupled to an automated rotater and ground on metallurgical lapping film (3 μm). Final preparations were superior to those made by hand on sintered glass with aluminum oxide, as the grind was finer and on a more even plane.

All prepared otoliths were examined and photographed at 500×–1250× under both white and ultraviolet light on a

Leitz Orthoplan fluorescence microscope with a 35-mm camera attachment. We used excitation filter bands from 450 to 490 nm and barrier filters at 510 and 515 nm.

To determine the position of the fluorescent band relative to the growth increments visible under white light, we photographed each otolith in a paired sequence: once under bright-field illumination and once under UV light. The otolith position and focus were not adjusted within a photograph pair sequence. Developed negatives were mounted directly into projector slides. Increment counts were made from the projected image. We defined an increment as a bipartite structure. Under transmitted light, it consisted of a narrow, opaque band and an adjacent wider, translucent region. Both major and total increment counts were made along the long axis of the sagittae. Major increments were generally easily distinguished on the basis of their continuity, intensity, and regularity of spacing. Minor increments differed, in that they often merged with other increments or were significantly lighter and thinner in appearance than the surrounding increments. The presence and spacing of increments in some otoliths was verified with a Perkin−Elmer Autoscan scanning electron microscope after etching the otoliths with 1% HCl for 90 s and coating with gold.

All counts were replicated at least three times in a random sequence by each author individually. Agreement within 10% between readers was considered acceptable and the mean taken; all questionable counts and/or preparations were removed from further analysis. These rejections comprised 3% and 9%, respectively, of the total number of otoliths.

Otolith anomalies that could conceivably affect the final increment count were noticeable in 10−20% of the light and electron microscopy photographs. These anomalies included the existence of multiple-growth foci leading to growth increments that merged with others and discontinuous increments. In two cases, these anomalies could have significantly altered the eventual increment count; these otoliths were rejected.

Results and Discussion

Tetracycline incorporation into the otolith was evident in 97% of the flounders injected. In each of those left alive at least a month after injection, the resulting fluorescent band spanned a minimum of five major increments and generally 14−20.

Incorporation into the otolith began in less than a day. A fluorescent band was visible in 50% of the fish, 10 h after injection, and in 100% of the fish, 24 h after injection. Therefore, the proximal edge of the band was considered to be located within one or two increments of the otolith periphery at the time of injection. A thin fluorescent line often associated with the ground otolith/glue interface was easily distinguishable from the fluorescence due to the tetracycline.

Both major and total increment counts were made from the proximal edge of the tetracycline band to the periphery of the otolith. Growth increments in left and right sagittae were counted separately for each fish. However, the mean of the two sagittae was used in the data analysis, as the two sides were not significantly different (95% confidence level). The width of the major increments varied between 0.9 and 3.4 μm, depending on the individual fish and location on the

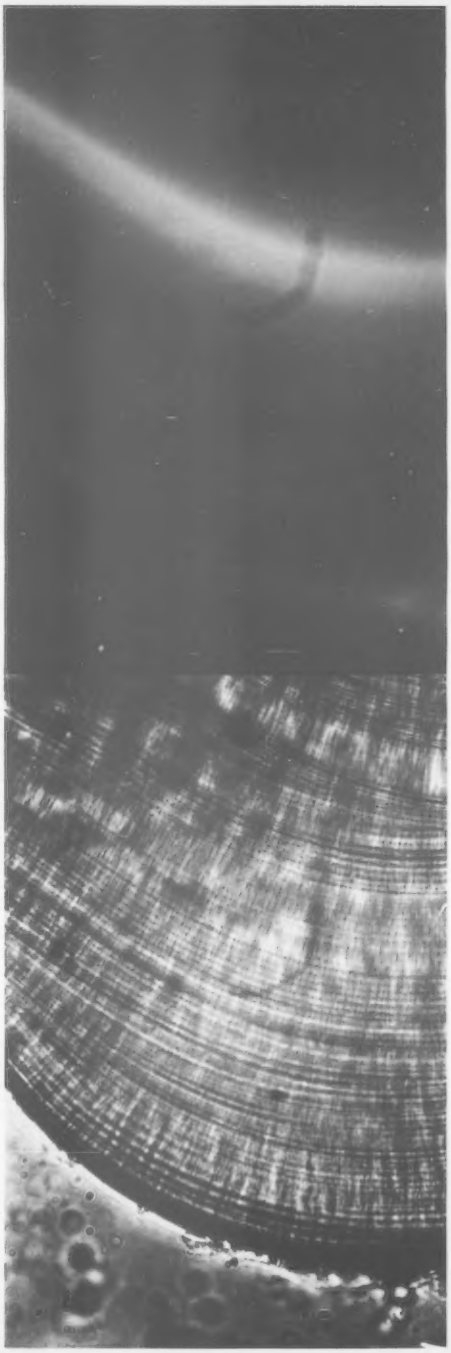

FIG. 1. (*Left*). Peripheral view of a ground, experimental starry flounder sagitta under bright field illumination; the daily growth increments are clearly visible. (*Right*). View of the same sagitta under ultraviolet light. The fluorescent band is due to incorporated tetracycline, whose location can now be associated with specific increments visible in *left* view. The flounder was sampled 45 d after tetracycline injection. Bar = 20 μm.

TABLE 1. Regression coefficient (b), standard error (SE), and corresponding R^2 value for the regression of major increment count on the number of days elapsed, for each of the experimental and in situ environments.

Expt.[a]	No. of fish	b	SE	R^2
In situ	13	1.06	0.06	0.96
13L:11D/CT	10	1.04	0.07	0.96
24L/CT	20	0.90	0.08	0.89
$24L/24T_1:12T_2$	16	0.90	0.06	0.93
24L:12D/CT	15	0.99	0.09	0.90
$24L:12D/24T_1:12T_2$	10	0.96	0.06	0.97

[a]L = light hours; D = dark hours; CT = constant temperature; $T_1 = 15°C$; $T_2 = 18°C$.

otolith. Minor increments numbered up to three between adjacent major increments; scanning electron microscope measurements indicated that these could be as narrow as 0.25 μm.

If the major growth increments on the otolith are laid down on a daily basis, a slope (b) of one should be obtained in the regression of major increment count on the number of days elapsed since tetracycline injection. All experimentally conditioned fish, as well as the fish maintained in situ, produced otoliths with a day:major increment slope not significantly different from one at the 95% confidence level (Table 1). We conclude that daily increments were laid down both in situ and in the experimental situations studied. Daily increments can be seen in the sagitta of Fig. 1. The major increments are daily, making the minor increments subdaily in nature. The laboratory data were then pooled as the slopes were not significantly different and Bartlett's test indicated homogeneity of variance between the experiments. Figure 2 shows the pooled laboratory daily increment data. The field data could not be pooled with the laboratory results, despite their similar slopes, because of the significantly lower variance of the former. The decreased variance was at least partially due to the relatively short time period between injection and sampling in situ. Both the field and laboratory results confirm a previously unverified observation of daily growth increments in starry flounders (Wilson and Larkin 1980).

Our results indicate that daily increments are formed in the sagittae of juvenile starry flounders under a variety of experimental conditions, as well as under a natural environment. This study also supports the view that unnatural light or temperature stimuli are not likely to induce a significant deviation from a natural daily increment pattern in postlarval fish preconditioned to a natural environmental regime. In starry flounders at least, laboratory observations of daily increment patterns in juveniles can probably be extrapolated to the natural situation.

The variance associated with the increment counts is somewhat higher than that reported in most previous publications. Although some of this may be attributable to reader error and poor otolith preparation, there appears to be a large species effect present in the integrity of increment deposition rate. Identical preparatory and reader counts made on threespine stickleback (*Gasterosteus aculeatus*) sagittae resulted in a much lower level of intraspecific variance (Campana unpublished data). This fact indicates that flounders produce an average of one increment per day, but large individual variations in production rates do occur. The reason for this variation is not clear, but does not appear to be common to many species.

Suggestions that temperature fluctuation (Brothers 1978) or photoperiod (Taubert and Coble 1977; Radtke 1978) might be the major factors controlling increment periodicity were not supported by our results. Thirty-six-hour "days" of the two conditions, even in conjunction, were ineffective in altering the production of one major otolith growth increment per 24 hours, averaged over a number of individuals. Similarly, constant temperatures and photoperiods had no visible effect on daily increment production indicating that neither environmental stimulus is mandatory for the maintenance of a 24-h periodicity in otolith growth, at least in flounders of several months of age. This is not to say that light or temperature can have no effect on increment deposition, but that a circadian rhythm is maintained despite their influence. It is possible that larval fish would be more susceptible to abnormal photoperiod or temperature cycles, as all of the flounders studied here were juveniles and therefore preconditioned to a natural light–dark cycle. If such were the case, these results would not be inconsistent with Taubert and Coble's (1977) observations. However, J. D. Neilson and G. H. Geen (1982, unpublished data) have reared chinook salmon (*Oncorhynchus tshawytscha*) eggs and alevins in total darkness and observed clear daily increment production in all cases.

The possibility that fish possess an internal, diel clock has been suggested before (Gibson et al. 1978; Eriksson and van Veen 1980). In mammals, endogenous 24-h rhythms are often entrained by a cyclic photoperiod, although a circadian rhythm persists under constant light or dark (Kramm 1980; Lynch et al. 1980). Taubert and Coble (1977) noted that larval sunfish (*Lepomis*) responded to an unnatural photoperiod by the production of nondaily growth increments that were not correlated with the relative "day" length. Therefore, they concluded that an endogenous biological clock, using photoperiod as a zeitgeber, was in operation. The results of our study differ, in that a 24-h periodicity in increment production was continued despite a 36-h photoperiod or constant light conditions. This inconsistency may be due to the different ages of the fishes used. However, our evidence does support the hypothesis that certain fish species possess an internally regulated circadian rhythm. The diurnal feeding and locomotory behavior in starry flounders supports this suggestion (Campana unpublished data). In addition, an endogenous periodicity is not contrary to the concept of variance associated with increment counts. Large individual variations in the expression of endogenous rhythms have been demonstrated in other fish species (Godin 1981).

A measure of the incidence of subdaily increments was given by total increment counts. A high degree of variability was associated with total counts, possibly resulting from the difficulty of viewing the subdaily increments and potential confusion with optical artifacts (Fig. 3). The slopes for the various experimental conditions using total counts were not significantly different (95% confidence level). However, the results did seem to indicate a high incidence of subdaily increments under a natural photoperiod regime (13L:11D/CT) ($b = 1.80$: SE = 0.24) and virtually none under conditions of constant light and temperature (24L/CT)

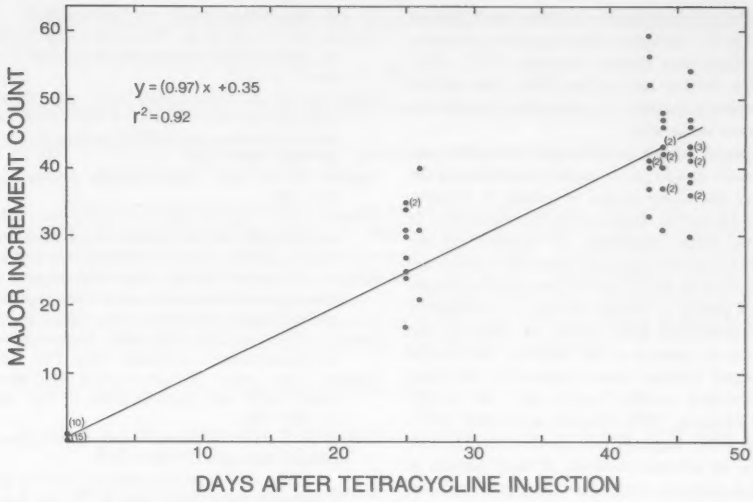

FIG. 2. Counts of major otolith growth increments distal to the origin of the fluorescent tetracycline band. Data are pooled from all laboratory environments.

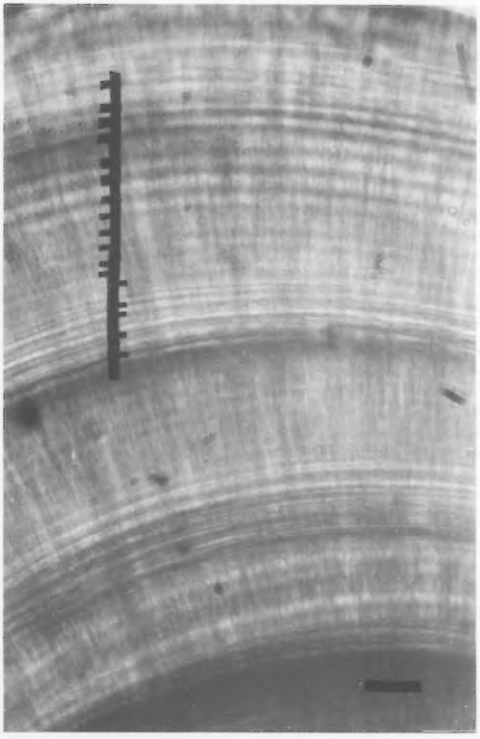

FIG. 3. Ground sagitta from an experimental starry flounder. Fine subdaily increments can be seen between the indicated daily increments. Bar = 10 μm.

(b = 0.99 : SE = 0.17). The in situ and other experimental fish were intermediate in their incidence of subdaily increments. Growth rates did not vary between experiments and therefore could not be implicated in the incidence of subdaily increments.

The variation in number of subdaily increments between experimental treatments was of interest. Although the difference was not significant by t-test ($0.05 < P < 0.10$), constant light conditions produced only 13% of the subdaily increments produced under a normal photoperiod. Subdaily increments were also observed in the fish kept in the outdoor enclosure. Subdaily patterns have been noted by other researchers (Taubert and Coble 1977; Brothers 1978), but the reasons behind their formation remain obscure. Both temperature cues (Brothers 1978) and feeding frequency (Neilson and Geen unpublished data) have been implicated in their formation.

The value of tetracycline for growth increment studies is enhanced by its rapid incorporation into the otolith, as reported here and elsewhere (Meunier and Boivin 1974). However, our results were not consistent with other observations of total incorporation over a single day in tuna (Wild and Foreman 1980). Tetracycline bands were generally 14–20 increments wide in this study; as sagittal growth occurs concentrically with increments added through time, tetracycline incorporation must be occurring over a 14- to 20-increment time period. Kobayashi et al. (1964) also noted that dual tetracycline injections remained distinct only when a month or more was alloted between applications. The discrepancy may be due to the higher metabolic rate of tuna relative to flounders and goldfish (*Carassius auratus*). Nevertheless, if the proximal edge of the band is accepted as corresponding to the date of injection, the width of the band is irrelevant, as the origin is accurately dated.

The tetracycline technique we used is one approach to confirming daily increment existence in wild fish, or in fish

of unknown age. Daily growth increments have been verified in only a few fish species. However, their occurrence has been suggested in numerous other species (Pannella 1971, 1974; Brothers et al. 1976; Wilson and Larkin 1980). The method outlined here provides a means of corroborating the occurrence of daily growth increments.

In those fish species where otolith daily increments are shown to exist, counts should prove useful in confirming the nature of annuli or spawning checks on scales or otoliths. Similarly, they can be used to determine the hatching dates of natural populations. Such information is valuable for the study of many species where spawning grounds or times are unknown. A precaution is necessary in that daily increment production may not persist in otoliths of older fish (Pannella 1974; Campana unpublished data). Also, the time of first increment formation in relation to the hatching date would have to be determined. Perhaps more importantly, the close correspondence between otolith length and fish length (Struhsaker and Uchiyama 1976; Taubert and Coble 1977; Wild and Foreman 1980) suggests that the distance between increments may be an accurate measure of daily growth in some cases. Such a measure would prove invaluable to the study of larval fish populations and is a suitable topic for future research.

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Selection of Bottom Type by Groundfishes of the Scotian Shelf

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SCOTT, J. S. 1982. Selection of bottom type by groundfishes of the Scotian Shelf. Can. J. Fish. Aquat. Sci. 39: 943–947.

Catches (numbers per tow) of 25 species of groundfish of the Scotian Shelf were estimated for five different bottom types on which the tows were made. An index of selectivity was calculated for each species. Selectivity ranged from highly specific in shallow-water species on sand and gravel bottom, to broad in deep-water species associated mainly with mud and silt bottoms, and in semipelagic species. Gradation in bottom-sediment particle size from northeast to southwest is correlated with clines in shallow-water fish abundance. Bottom type and water depth are correlated with each other and with fish distribution.

Key words: bottom type, groundfish, sediment type

SCOTT, J. S. 1982. Selection of bottom type by groundfishes of the Scotian Shelf. Can. J. Fish. Aquat. Sci. 39: 943–947.

Nous avons estimé les prises (en nombres par trait de chalut) de 25 espèces de poissons de fond du plateau Scotian sur cinq types de fond différents. Pour chaque espèce, nous avons calculé un indice de sélectivité. Cette dernière varie de fortement spécifique chez les espèces d'eau peu profonde sur fonds de sable et gravier à étendue chez les espèces d'eau profonde se rencontrant surtout sur fonds de vase et de limon, et chez les espèces semi-pélagiques. Il y a corrélation entre la taille des particules du sédiment benthique, du nord-est au sud-ouest, et les gradients d'abondance des poissons en eau peu profonde. Il en est de même entre types de fond et profondeur de l'eau d'une part et la distribution des poissons d'autre part.

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GEOGRAPHICAL distribution of fishes is determined by a number of factors which may vary between species, food being one of the major factors. Different groundfishes have different food preferences in the northwest Atlantic, as elsewhere (Langton and Bowman 1980), and it seems reasonable to assume that the availability of preferred prey plays an important part in determining characteristic distributions of the fish stocks of the Scotian Shelf (Scott 1976). A further assumption may be made that the availability and distribution of benthic and epibenthic organisms which constitute much of the diet of groundfishes are determined by the nature of the sea bottom in or on which they live (Gray 1974); each bottom type should support a typical invertebrate faunal assemblage which, in turn, should support a characteristic fish fauna.

Catches of groundfishes in relation to the surficial geology of the Scotian Shelf are examined here to test the hypothesis that groundfish distributions are correlated with bottom type. Such correlation could be used as a basis for designing groundfish research surveys as an alternative to the depth-stratified survey designs used at present in the northwest Atlantic.

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Materials and Methods

Since 1970 the Marine Fish Division, Scotia-Fundy (formerly Maritimes Region), has carried out annual summer research trawl surveys for groundfish on the Scotian Shelf. Standard vessel, gear, and length of tow are used and, for each set, position, depth, number, and weight of each fish species caught are recorded. For the period 1970–76, 1007 sets were made, distributed fairly evenly over the Shelf (Fig. 1), each of which was correlated with the sediment type of the sea bottom on which the tow was made, using known position of tow and maps of the surficial geology of the Scotian Shelf (King 1970; MacLean and King 1971; Drapeau and King 1972; Fader et al. 1977). Five major sediment (bottom) types were identified from the maps, and for each type the mean number per tow for each of the 24 more common groundfishes and squid was calculated (Table 1). With the exception of "Scotian Shelf drift," a variable deposit which could not be fitted into the sequence, the bottom types, in order of decreasing grain size, are (1) Sable Island sand and gravel; (2) Sambro sand; (3) Emerald silt; (4) LaHave clay; (5) Scotian Shelf drift: glacial till, may include some stratified drift on outer shelf.

In general, the typical deposit on the Nova Scotia banks is Sable Island sand and gravel, occupying almost all areas

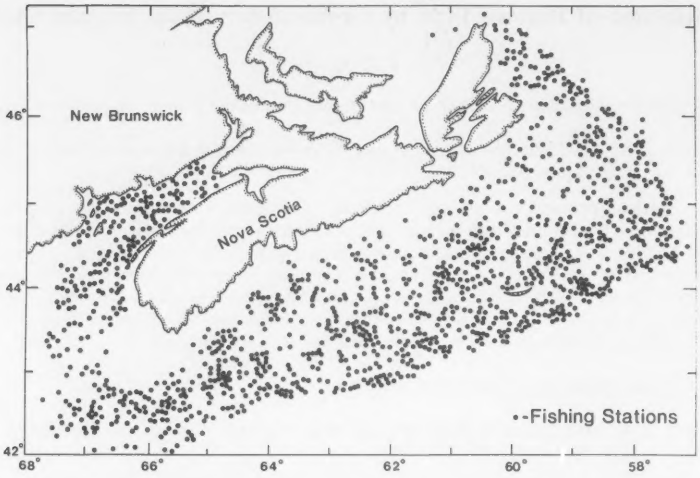

FIG. 1. The Scotian Shelf showing fishing stations related to bottom type, 1970–79.

under 91 m (50 fath) in depth. Sambro sand lies in intermediate depths on the Scotian Shelf between adjacent banks and on the edges of the basins. It is also the typical deposit in the deeper water on the edge of the Continental Shelf. Emerald silt is characteristic of the slopes of the deep-water basins in the Shelf and LaHave clay occupies the bottoms of the basins. Scotian Shelf drift is a variable deposit, including gravels, silts, clays, and boulders, and occurs at various depths. Details of each facies are given with the geological maps referred to above.

For estimation of the degree of selectivity of each fish species for bottom type, an index of preference was calculated: number of bottom types in which percentage frequency of occurrence of the fish (percent mean number per tow) exceeds 10% of the maximum percent frequency of occurrence in the range shown by the species against the five bottom types, e.g. Argentine (Table 1) — mean catch per tow per bottom type: 0.04, 0.31, 0.84, 0.06, 0.79; maximum = 0.84; 10% level = 0.08; index = number of bottom types in which mean catch exceeds 0.08 = 3 (bottom types 2, 3, 5). The 10% level was selected more or less subjectively because 30 and 50% gave too low a spread of indices and 0% too little discrimination. Using this index, the fish were arranged in descending order of site-specificity and, within each group with the same index, in descending order of correspondence with bottom types ranked by particle size (Table 1).

Relationship of bottom type to water depths was examined by comparing bottom type for each tow with the recorded depth of tow.

Results

Comparison of selectivity indices with sediment type (Table 1) showed that, coincident with decreasing specificity from 1 to 5, there was a change in bottom-type preference from coarser sand and gravel to finer sediments. Mean catches per tow were on the whole higher in the latter, with redfish and silver hake far outnumbering the typical shallow-water species, yellowtail flounder and sand lance, although catches of sand lance may be badly underestimated because of the fish's low catchability.

With the exception of argentine, ocean pout, and longfin hake, which favored silty bottom, fishes in index categories 1–3 showed strong preferences for substrates with a high proportion of sand or gravel such as are found in relatively shallow water on the Scotian Shelf. The remainder of fishes in these categories showed comparatively little specificity, but even in these there were indications of bottom-type preference (Table 1). In the largest category, index 4, haddock, wolffish, and plaice showed strong association with coarser, sandy sediments and steadily diminishing catch rates as the bottom tended to silt and clay. Cusk selected finer deposits, silver hake was well distributed with a moderate preference for deposits in silt–sand and silty bottoms of the midrange of sediments, and spiny dogfish was associated mainly with rather coarser bottoms. Redfish was very poorly represented on the coarser sediments, but increased through the midrange to peak in the fine-grained bottom of the LaHave clayey–silt facies. White hake also showed the strongest preference for fine-grained sediments. It was absent from the gravel and sands of the Sable Island facies, but catch rates increased in finer deposits to peak on the clays of the Lahave facies.

In category 5 the fishes were well represented over a wide variety of bottom types, but again showed distinctive preferences. Catch rates of cod and thorny skate were highest on the coarser-grained sediments and diminished as grain size decreased; witch flounder showed the opposite trend, favoring the silty and clay bottoms.

Squid showed a slight preference for the mixed sand–silt bottom of the Sambro sand facies but, like angler and pollock, which were the least specific to bottom type of the fishes studied, showed little preference for special bottom types. Angler and pollock were associated with sediments ranging from gravels to clay, angler giving highest catch rate in the

TABLE 1. Indices of preference and mean catch (number) per tow of groundfishes by bottom type on the Scotian Shelf. 1, Sable Is. sand and gravel; 2, Sambro sand; 3, Emerald silt; 4, LaHave clay; 5, Scotian Shelf drift.

Species	Index	Bottom type				
		1	2	3	4	5
Northern sand lance *Ammodytes dubius*	1	17.36	—	—	—	—
Yellow flounder *Limanda ferruginea*	1	16.74	0.52	—	—	0.21
Winter skate *Raja ocellata*	2	0.52	0.05	—	—	0.03
Longhorn sculpin *Myoxocephalus octodecemspinosus*	2	2.46	0.29	—	—	0.15
Atlantic halibut *Hippoglossus hippoglossus*	2	0.10	—	0.14	—	—
Ocean pout *Macrozoarces americanus*	2	—	—	0.20	—	0.03
Winter flounder *Pseudopleuronectes americanus*	3	0.38	0.15	—	—	0.14
Smooth skate *Raja senta*	3	—	0.25	0.10	—	0.07
Sea raven *Hemitripterus americanus*	3	0.08	0.20	—	—	0.16
Argentine, Atlantic *Argentina silus*	3	0.04	0.31	0.84	0.06	0.79
Longfin hake *Physis chesteri*	3	—	0.62	—	0.45	0.95
Haddock *Melanogrammus aeglefinus*	4	7.73	4.89	1.18	0.21	0.98
Atlantic wolffish *Anarhichas lupus*	4	0.22	0.15	0.07	—	0.06
American plaice *Hippoglossoides platessoides*	4	10.13	6.07	5.90	4.92	0.84
White hake *Urophycis tenuis*	4	0.08	2.02	1.17	3.75	2.47
Redfish *Sebastes* spp.	4	1.33	17.90	27.86	66.28	61.06
Cusk *Brosme brosme*	4	0.02	0.30	0.15	0.07	0.24
Spiny dogfish *Squalus acanthias*	4	0.08	1.74	1.44	0.94	3.98
Silver hake *Merluccius bilinearis*	4	1.40	4.41	18.47	13.21	3.77
Thorny skate *Raja radiata*	5	2.90	1.22	0.83	0.55	0.78
Atlantic cod *Gadus morhua*	5	8.70	2.47	2.63	0.85	2.35
Short-finned squid *Illex illecebrosus*	5	2.37	18.48	5.84	14.29	15.83
Witch flounder *Glyptocephalus cynoglossus*	5	0.20	0.71	1.04	1.28	1.49
Angler (goosefish) *Lophius americanus*	5	0.08	0.10	0.14	0.22	0.17
Pollock *Pollachius virens*	5	0.37	0.54	0.42	0.38	1.18
Number of species		22	22	18	15	23

finest deposits and pollock in the midrange, but showed no trend associated with grain size.

The numbers of fish species associated with each bottom type fell into groups (Table 1). The mixed bottom of the Scotian Shelf drift supported most species (23) as would be expected from an environment offering a wide range of ecological niches. It was closely followed by the sandy deposits (22). The silt (18) and clay (15) bottoms were comparatively poorer in fish species although catch rates of redfish and silver hake were among the highest found.

There was good correlation between bottom type and water depth (Fig. 2). This was evident both from the statistical data

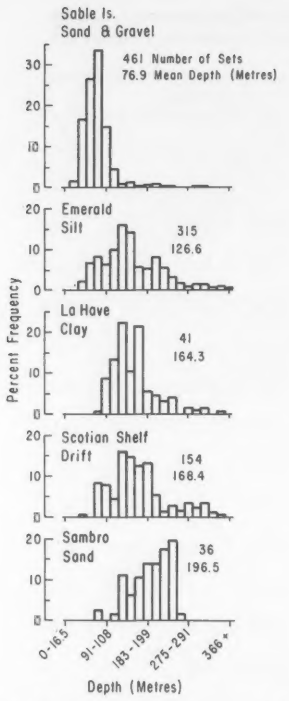

FIG. 2. Depth distributions of bottom types on the Scotian Shelf.

and from inspection of the maps of surficial deposits. The strongest correlation was in shallow water where sands and gravels of the Sable Island facies were virtually limited to a depth range of 0 (Sable Island) to 110 m (0–60 fath). The remainder of the bottom types showed a wider depth distribution, but mean depths increased through the sequence Emerald silt, LaHave clay, Scotian Shelf drift (a mixed facies without the comparative uniformity of the other sediments) to Sambro sand.

Discussion

The wide range of bottom-type specificities shown by the different groundfishes and squid of the Scotian Shelf indicates that site selection is a significant factor in determining differential distribution, but this varies in specificity between fish species. There is obviously wide overlap between many fishes — 25 major species distributed among five bottom types demands this — but even within groups of fishes with similar overall distributions there are differences in degree of preference for various substrates. This is particularly well illustrated if groups of related fish are considered.

In the Pleuronectidae (flatfishes) there is progressive preference from coarse-to-fine sediments in the sequence yellowtail flounder, winter flounder, American plaice, witch flounder (Table 1). Yellowtail flounder is virtually confined to the Sable Island sand; winter flounder extends from the sand to sand–mud bottom; plaice occupies almost all facies from gravel to clay, but is concentrated on sands, gravels, and sand–silt; and witch, rare on the sands and gravels, is concentrated on silts and clays.

A similar progression is found in the Gadidae (cod-like fishes). Preferences are less well defined here than in the flatfishes as all members of the group are associated with a wide range of sediments. Cod and haddock show remarkably similar distributions, as expected from their close association in catches. They are most highly concentrated in the sand–gravel facies, but the more varied diet of cod (Langton and Bowman 1980) is reflected in its lower selectivity for bottom type. Cusk is concentrated on the silt–sand bottoms of the Sambro sand facies and the broken bottom of the Scotian Shelf drift, while silver hake is mainly found associated with the silts and clays of the Emerald and LaHave facies. White hake and longfin hake show similar preferences, being most strongly associated with the Sambro sand, LaHave clay, and Scotian drift facies, but, whereas white hake is also associated with the remaining sediment types to a lesser extent, longfin hake is restricted to the three main facies.

A third group, Rajidae (skates), again shows strong diversity. Winter skate is confined to sands and gravels, thorny skate is widespread but is mainly concentrated from sandy bottom of the Sable Island facies to the sandy silt and clay of the LaHave facies, and smooth skate is restricted to the finer sediments.

There are numerous references to the relationship between bottom type and depth in the texts accompanying the various maps of surficial deposits referred to above. The sequence of bottom types in relation to depth is largely due to glacial action and change in sea level some 15 000–19 000 yr ago (King 1970) with a secondary, more recent, sorting effect of water currents on the sediments. The relatively coarse sands and gravels, such as the Sable Island facies, are associated with shallow water and the finer deposits with deeper water, more or less in relation to grain size. Sambro sand, a mixture of fine sand and silt, characterizes both intermediate depths between the banks and deep basins on the Shelf. It also characterizes the edge of the Continental Shelf between the banks and the greater depths of the Continental Slope, the deepest area trawled. Therefore, it appears as the deposit with the greatest mean depth. Emerald silt is associated with deep water and usually lies on the lower slopes of the basins between the Sambro sand and LaHave clay facies. Scotian Shelf drift, a mixed deposit "containing angular fragments in the pebble, cobble and boulder range . . . dominantly sandy but everywhere contains abundant silt and clay" (Drapeau and King 1972) does not fall readily into the sequence. It offers all types of bottom and obviously cannot be regarded as a single sediment type to the same degree as the others.

There is an east-to-west change in bottom type on the Scotian Shelf, involving increase in the proportion of gravel in the sediments on the banks (Drapeau and King 1972). This may be correlated with changes in fish distribution. Several species strongly associated with sand–gravel bottom (e.g. haddock, cod, plaice, yellowtail flounder, thorny skate) show obvious changes in abundance from east to west (Scott 1976). These changes in concentration have been related to temperature (Scott 1976), but differences in grain size may be a contributory or even determining factor.

Having considered the relationships of fish distribution to

each of the parameters, bottom type and water depth, there remains the question as to which, if either, is the more basic factor in determining where fish will occur.

At first sight, depth appears to be the less likely determinant. Most groundfishes of the Scotian Shelf are found over wide depth ranges, which may vary seasonally depending on such factors as water temperature, spawning requirements, and prey concentrations. For instance, cod range from deep water between the banks to shallow inshore waters, haddock and plaice move on and off the banks, silver hake migrate from deep water off the Shelf to the shallows of Sable Island to spawn, and pollock range from coastal waters to great depths in the Shelf and gullies at the edge of the Shelf.

There are some species, however, which do not show extensive seasonal movements, including yellowtail flounder, sand lance, winter skate, longhorn sculpin, sea raven (Bigelow and Schroeder 1953), and probably longfin hake and argentine. It may be significant that these species exhibit high selectivity for bottom type and that the five former fishes favor shallow waters (Scott 1972) with large temperature ranges. Also, the major concentrations of yellowtail, sand lance, and winter skate are in the northeast part of the Shelf in shallow water in similar depth ranges to those found on the banks in the southwest, but associated with the less gravelly bottoms to the northeast. Bottom type rather than depth appears more important, therefore, in determining distribution in these species. Longfin hake and argentine are deep-water fishes, concentrated along the edge of the Shelf in waters of stable temperature, on mud or silt bottoms, mostly in depths over 183 m (100 fath), so it is difficult to select from the restricted environment any one factor which determines their occurrence.

Halibut and smooth skate have relatively low selectivity indices, are widely distributed over an extensive depth range on the Shelf, and are closely associated with the bottom. Bottom type seems more important than depth in their distribution.

The remainder of the species listed in Table 1 show relatively low preference for bottom type. This is unexpected in the cases of wolffish which feed on molluscs, crustaceans, and sea urchins; haddock, a benthos feeder; and on the bottom dwellers thorny skate, plaice, and witch flounder. Each shows some degree of specificity: wolffish and haddock for sands and gravels, thorny skate and plaice for sandy silts, and witch for silts and clays, but their prey is not specific to a narrow range of bottom types (Bigelow and Schroeder 1953), nor are the fish limited to a narrow depth range (Scott 1972), so neither bottom type nor depth acts as a specific determinant of distribution.

Similarly, the feeding habits of short-finned squid and pollock, mainly on fish and pelagic crustaceans, are the least bottom-oriented of all the species considered, in accordance with their low selectivity. Anglers, also, show little preference for bottom type, and take advantage of any substrate over which its fish prey occurs.

The similarity in bottom-type preferences between cod and haddock (Fig. 1) is surprising in view of the difference in diets, but corresponds to the close association between the species as indicated by trawl catches (J. S. Scott unpublished data). In contrast to the largely benthic feeding of haddock, cod feed largely on fish (Langton and Bowman 1980) and the cod's fairly high preference for sand and gravel bottom (Table 1), similar to the haddock's, may reflect a secondary effect of bottom preference: the fish on which cod feed, including sand lance, in particular, and probably young haddock, are oriented towards sand or gravel bottom, attracting cod which, in turn, reflects the preference of the prey.

In summary, there is evidence that several species of groundfishes are highly selective for bottom type. In others, the correlation between occurrence, bottom type, depth, and temperature, all possibly affecting the distribution of benthic prey on the Scotian Shelf, makes it difficult to select a major determinant, if any, from the complex of factors. The lowest correlation of occurrence with bottom type is shown by species which have largely pelagic or semipelagic feeding habits, again an indication that specificity for bottom type may be related to the occurrence of prey organisms associated with particular substrates.

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Vitamin C and Disease Resistance in Channel Catfish (*Ictalurus punctatus*)

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DURVE, V. S., AND R. T. LOVELL. 1982. Vitamin C and disease resistance in channel catfish (*Ictalurus punctatus*). Can. J. Fish. Aquat. Sci. 39: 948–951.

Channel catfish (*Ictalurus punctatus*) fingerlings were fed semipurified diets containing 0–150 mg/kg of vitamin C for 14 wk and subsequently at two temperature regimes infected with the pathogenic bacterium *Edwardsiella tarda*. Mortality rates were determined 96 h after infection. A supplemental vitamin C level of 30 mg/kg of diet was sufficient for normal growth and for prevention of deficiency signs such as lordosis, scoliosis, and a reduction in bone collagen formation. However, increased resistance against infection was provided when the level of supplemental vitamin C was increased to the highest dietary level, 150 mg/kg, at a water temperature of 23°C. At 33°C, increasing the supplemental level of vitamin C had significantly less effect on resistance against infection. The difference in response at the two temperatures indicates that the vitamin C requirement for resistance to infection is possibly higher when channel catfish are infected at lower temperatures, where the natural resistance is reduced, than when infected at a temperature near optimum for the natural resistance mechanisms of the fish.

Key words: vitamin C, channel catfish, disease resistance, *Edwardsiella tarda*, infection

DURVE, V. S., AND R. T. LOVELL. 1982. Vitamin C and disease resistance in channel catfish (*Ictalurus punctatus*). Can. J. Fish. Aquat. Sci. 39: 948–951.

Des fingerlings de barbue de rivière (*Ictalurus punctatus*) ont été nourris à des régimes semi-purifiés contenant de 0 à 150 mg/kg de vitamine C durant 14 sem et ensuite infectés, à deux régimes thermiques, par la bactérie pathogène *Edwardsiella tarda*. Les taux de mortalité ont été déterminés 96 h après l'infection. Un supplément de vitamine C de 30 mg/kg de nourriture suffit à assurer une croissance normale et à prévenir des signes de déficience tels que la lordose, la scoliose et une formation diminuée de collagène des os. Cependant, la résistance à l'infection est plus grande si l'on élève au maximum le niveau de vitamine C, soit 150 mg/kg, à une température de l'eau de 23°C. A 33°C, l'augmentation de vitamine C a un effet nettement moindre sur la résistance à l'infection. Cette différence de réponse aux deux températures indique que, pour résister à l'infection, il faut un niveau plus élevé de vitamine C quand les barbues sont infectées à de basses températures alors que la résistance naturelle est amoindrie, que quand les poissons le sont à une température à peu près optimale pour les mécanismes de résistance naturels.

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FISH are highly sensitive to a dietary adequacy of vitamin C. Deficiencies have caused reduced growth rate, deformation of skeletal and cartilagenous tissues, capillary fragility, slow wound repair, and increased rate of mortality (Kitamura et al. 1965; Halver et al. 1969; Lovell 1973; Wilson 1973; Lim and Lovell 1978). Vitamin C-deprived channel catfish (*Ictalurus punctatus*) have an increased susceptibility to bacterial diseases (Lovell 1973; Lim and Lovell 1978). However, we had no information on the effect of elevated levels of vitamin C, levels above that required for normal growth and prevention of clinical deficiency signs, on resistance to infectious disease in fish. Beneficial effects of elevated levels of vitamin C on resistance to infection have, however, been reported for humans and guinea pigs. Leucocyte responses in humans (Delafuente et al. 1979) and lymphocyte activity in guinea pigs (Fraser et al. 1980) increased in dose response fashion when up to 10 times the normal dietary requirement of vitamin C was given prior to challenge with various antigens. Also, megalevel doses of the essential vitamins A and E have increased the protection of mice (Heinzerling et al. 1974) and chickens (Tengerdy and Nockels 1975) against pathogenic bacteria.

The purpose of our study was to determine the effect of elevated levels of dietary vitamin C on the resistance of channel catfish to the pathogenic bacterium *Edwardsiella tarda*.

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TABLE 1. Composition of purified basal diet to which various levels of vitamin C were added to replace cellulose.

Ingredients	Percentage
Vitamin-free casein	32.6
Gelatin	9.4
Dextrin	33.05
Cellulose	10.0
Carboxymethyl cellulose	3.0
Soybean oil	4.0
Cod liver oil[a]	3.0
Mineral mix[b]	4.0
Ascorbic acid-free vitamin mix[c]	0.95

[a]Cod liver oil contained 850 IU of vitamin A per gram and 85 ICU of vitamin D per gram.

[b]Mineral mixture of Williams and Briggs (1963) supplemented with cobalt chloride (1 mg/kg of diet), aluminum potassium sulfate (0.7 mg/kg of diet), and sodium selenite (0.08 mg/kg of diet).

[c]Provided the following diluted in cellulose (mg/kg of diet): thiamin, 10; riboflavin, 20; pyridoxine, 10; folic acid, 5; Ca pantothenate 40; choline chloride, 3000; niacin, 150; vitamin B_{12}, 0.06; retinyl acetate (500 000 IU/g), 12; alpha tocopherol, 50; cholecalciferol (1 000 000 ICU/g), 6; menadione-Na-bisulfite, 80; inositol, 400; biotin, 2; ethoxyquin, 200.

Methods

Channel catfish fingerlings (weighing ~ 4 g) of the Auburn strain were fed four purified diets (Table 1) containing 36% protein and 12.1 kJ of digestible energy per gram and 0, 30, 60, or 150 mg/kg of supplemental vitamin C (U.S.P. grade L-ascorbic acid) for 18 wk. Each diet was fed to three replicate groups of 40 fish stocked in 60-L glass aquaria with continuously flowing (0.8 L/min), charcoal-filtered water from the city water system, maintained at 29 ± 1°C. The fish were fed in two feedings daily (08:00 and 17:00) at a rate equal to 2.8% (dry matter basis) of the weight of the fish. Feeding regimes were adjusted every 2 wk. The inside of the aquaria was brushed semiweekly to minimize algal and fungal growth which could provide a source of ascorbic acid. At biweekly intervals when the fish were removed for weighing, the aquaria were emptied and scrubbed thoroughly.

The diets were mixed, wetted to 27% moisture, and extruded into 1.6-mm-diameter by 3-mm-length pellets with a food grinder (model 12, Hobart, Inc., Columbus, GA). The pellets were hermetically sealed in flexible pouches and frozen quickly after extrusion. The diets were stored at −23°C and periodically a 1-wk allowance was transferred to a refrigerator (3°C) and held until fed. Periodic measurement of ascorbic acid in the diets, using a modification of the method of Vuilleumeir and Nobile (1962) as described by Lovell and Lim (1978), indicated only slight loss of ascorbic acid activity (less than 5% at 10 wk) in the diets during storage.

After 14 wk of feeding, when lordosis and scoliosis were first observed among fish fed the vitamin C-free diets, 80 fish from each dietary treatment were randomly divided into two groups of equal numbers. The fish from one group in each treatment were restocked in aquaria at 23°C and the fish in the other group were restocked at 33°C. After acclimation to the changed water temperatures for 96 h, one-half of the fish at each water temperature was infected with a virulent strain of the pathogenic bacterium *E. tarda*, and the other half served as controls.

The *E. tarda* strain was isolated from channel catfish in Kentucky in 1979 and maintained in stock culture in the Fish Disease Diagnostic Laboratory at Auburn University. Before the fish in this study were infected, the *E. tarda* cells were cycled through channel catfish to enhance their virulence. This was done by transferring cells from the stock culture to freshly prepared brain-heart infection (BHI) agar (DIFCO Laboratories, Detroit, MI) plates, growing them for 18 h at 32°C, harvesting the fresh cells in 0.85% saline solution, and injecting 0.1 mL of a suspension containing 10^4 cells/mL intraperitoneally (i.p.) into 15-g channel catfish. After 96 h, the posterior kidneys of these fish were removed and homogenized in 10 volumes of sterile saline, and the homogenate was streaked on BHI agar plates. After two cycles through channel catfish, 0.1 mL of a cell suspension, containing 10^4 cells/mL, was injected into each of the experimentally infected fish. A preliminary exercise showed that an i.p. injection of these cells at this concentration would cause 50 to 100% mortality in 15-g channel catfish, fed 30 mg of vitamin C per kilogram of diet, within 96 h at 29°C. The control fish were injected with 0.1 L of of the sterile saline solution. Prior to injection the fish were anesthetized by placing them in water containing 50 mg/L of quinaldine for a few minutes. After infection the fish were placed in aquaria with flowing water at the prescribed temperatures.

When the fish were infected at 14 wk, three fish were sampled from each aquarium for analysis for ascorbic acid in the liver and collagen in the vertebrae. Livers were analyzed from individual fish by the method of Polk et al. (1960). Vertebral collagen percentage was determined by a procedure described by Lim and Lovell (1978). Thirty fish in each dietary treatment were fed for an additional 4 wk to compare further growth rates. Growth, liver ascorbic acid, and vertebral collagen data were analyzed for statistical differences among treatment means by Duncan's (1955) new multiple range test following analysis of variance. Significant differences in mortality rates among infected fish were determined with the binomial test by comparing the 95% confidence interval for percentage mortality for each treatment (Conover 1971). If intervals overlapped, the mortality rates were not different at $P \leq 0.05$.

Results

Signs of vitamin C deficiency, such as scoliosis and lordosis, were first found in the fish fed the vitamin C-free diet after 14 wk. This was used as the signal that the fish were scorbutic. There was no difference in growth rate among treatments at this time (Table 2); however, rate of food consumption had begun to decline for fish fed the vitamin C-deficient diet and by the 18th week these fish were significantly smaller than those in the other groups. The lowest dietary level of vitamin C, 30 mg/kg, was adequate for normal bone collagen formation (Table 2), but 60 mg/kg was necessary for a satisfactory liver level of vitamin C. Lim and Lovell (1978) found that bone collagen below 29.5% indicated impaired collagen formation, and that a liver level below 30 mg of vitamin C per gram of wet tissue was indicative of scorbutic channel catfish.

TABLE 2. Accumulative weight gain, incidence of scoliosis and lordosis, level of liver vitamin C, and amount of collagen in vertebrae in channel catfish fed various dietary levels of vitamin C for 14 wk.[1]

Dietary level of vitamin C, mg/kg	Weight gain, g	Deformed fish, %	Liver vitamin C, μg/g	Vertebral collagen, %
0	12.5[a]	9	13.3[a]	23.1[a]
30	13.1[a]	0	18.1[a]	30.2[b]
60	11.5[a]	0	45.0[b]	29.4[b]
150	13.9[a]	0	80.0[c]	29.3[b]
Pooled SD	3.2		5.6	1.0
P level[2]	ns		0.05	0.01

[1]Average weight gain and percentage deformed fish are from three aquaria of 30 fish each: values for liver vitamin C and bone collagen are average of five fish from each of three aquaria.

[2]Probability level at which treatment effects are significantly different; means in a column sharing a common superscript letter are not significantly different (ns).

At the lower postinfection temperature, 23°C, all infected fish fed the vitamin C-free diet died within 96 h (Table 3). Mortality rate among fish fed diets containing 30 mg/kg of vitamin C was not significantly lower than that of the fish fed the vitamin C-free diet. Mortality rate among fish fed 60 mg/kg of vitamin C was significantly lower than that of fish fed the vitamin C-free diet, but significantly higher than that of the fish fed 150 mg/kg of vitamin C. All mortalities among infected fish showed clinical signs of *E. tarda* infection: depigmented areas of skin on the dorsal part of the body, gas pockets beneath the skin, and inflamed areas beneath the mouth. Two fish died in each of two noninfected (saline injected) groups; however, the dead fish did not show signs of *E. tarda* infection.

At 33°C, mortality rate was only 50% among infected fish fed the vitamin C-free diet (Table 3). Mortality rate for fish fed 30 and 60 mg of vitamin C per kilogram of diet was not significantly different from that of the scorbutic fish. Mortality rate at the 150 mg/kg vitamin C level was significantly lower than that of the fish fed the vitamin C-free diet, but not lower than those of the fish fed 30 or 60 mg of the vitamin per kilogram of diet. Infected fish from each dietary treatment had significantly higher mortality rates at 23°C than at 33°C except at the highest vitamin C level where there was no between temperature difference.

Discussion

Our study indicates that levels of vitamin C higher than the minimum dietary requirement for normal growth and bone development provided increased resistance to *E. tarda* infection in channel catfish held at 23°C. A level of 30 mg of vitamin C per kilogram of diet was adequate for normal growth and bone development and 60 mg/kg maintained normal liver levels of vitamin C; however, up to five times the requirement for normal growth was effective in reducing mortalities caused by *E. tarda* infection. Previous studies with channel catfish showed that 30 mg/kg was adequate for normal growth and to prevent scoliosis and lordosis, but 60 mg/kg was necessary for maximum rate of wound repair (Lim and Lovell 1978). In rainbow trout (*Salmo gairdneri*), 100 mg/kg was sufficient for normal growth, but 1000 mg/kg provided maximum rate of wound repair (Halver et al. 1975). This indicates that the nutritional requirement for vitamin C by fish varies with metabolic function. From our study, it appears that resistance to bacterial infection increases with an increase in dosage of vitamin C, especially at temperatures around 23°C. We do not know if levels higher than 150 mg/kg would further increase resistance to infection.

The apparent increase in vitamin C requirement subsequent to *E. tarda* infection could be related to several mechanisms. One possibility is that the increase in leucocyte or phagocytic activity following infection increased vitamin C requirement. Thomas and Holt (1978) reported that the high concentration of L-ascorbic acid in human leucocytes rapidly decreased during infection as phagocytosis increased. Raising the level of dietary vitamin C improved macrophage migration in guinea pigs (Ganguly et al. 1976). Lymphocyte activity, measured by DNA synthesis in humans (Delafuente et al. 1979) and uptake of tritiated thymidine in guinea pigs (Fraser et al. 1980), increased with greater doses of vitamin C. Both phagocytosis and antibody production were increased by feeding higher than normal levels of vitamins E or A to mice (Heinzerling et al. 1974) and chickens (Tengerdy and Nockels 1975) prior to infection with pathogenic bacteria. Law and Nockels (1976) found an increase in antibody production in chickens fed vitamin C prior to infection with Newcastle

TABLE 3. Mortality rates (96 h) of channel catfish fed various dietary levels of vitamin C and subsequently infected with *Edwardsiella tarda* at two water temperatures.

Dietary level of vitamin C, mg/kg	23°C				33°C			
	Infected	No. deaths /no. fish infected	%[1]	95% confidence interval	Infected	No. deaths /no. fish infected	%[1]	95% confidence interval
0	+	20/20	100[a]	85–100	+	10/20	50[a]	33–71
	−	2/20	10[b]	1–30	−	0/20	0[b]	0–15
30	+	17/20	85[ac]	64–69	+	4/20	20[abc]	7–40
	−	0/20	0[b]	0–15	−	0/20	0[b]	0–15
60	+	12/20	60[c]	0–15	+	4/20	20[abc]	7–40
	−	2/20	10[b]	1–30	−	0/20	0[bc]	0–15
150	+	4/20	20[db]	7–40	+	2/20	10[bc]	1–30
	−	0/20	0[b]	0–15	−	0/20	0[b]	0–15

[1]Means in a column sharing a common superscript letter, indicating overlapping 95% confidence intervals, are not significantly different at $P \leq 0.05$.

vaccine. Antibody production, however, was probably not responsible for the increased resistance of the channel catfish receiving elevated doses of vitamin C because mortality rate was measured over a 96-h period and protection from antibody production or other acquired immune responses would require a longer period.

Another possible mechanism for increased resistance related to elevated vitamin C may concern the positive relationship between dietary dose of vitamin C and synthesis and release of glucocorticoids by the adrenal gland (Kitabachi 1967; Wilbur and Walker 1978). Interrenal ascorbic acid decreased and plasma cortisol increased in rainbow trout (Wedemeyer 1969) and channel catfish (Strange et al. 1977) when the fish were stressed. Also, the effect of vitamin C on iron metabolism, by interconversion of ferric to ferrous iron for plasma transport and cellular absorption (Lipschitz et al. 1971), may be a clue to the relationship between disease resistance and elevated doses of vitamin C in channel catfish. Plasma iron concentration and iron saturation of transferrin in the host animal have been associated with pathogenicity of infectious bacteria (Weinberg 1971).

Elevated dietary levels of vitamin C were less effective in increasing resistance of the fish against *E. tarda* at 33°C than 23°C. Rasheed (1978) showed that natural resistance of nonstressed channel catfish to bacterial infection (*A. hydrophila*) decreased as temperature increased from 10 to 20°C, then increased with a further increase in temperature from 20 to 30°C. Avtalion (1981) reported similar responses in other warmwater fishes and offered the explanation that the pathogenicity of the bacterium increased faster than the resistance of the host up to ~20°C, but as temperature increased toward the fish's optimum growth temperature, the reverse occurred. Thus, our study indicates that the benefit of feeding elevated levels of vitamin C to increase resistance against *E. tarda* infection is minimal at temperatures that are optimum for the resistance mechanisms of the fish. At lower temperatures, where resistance mechanisms are less responsive to infection, channel catfish respond favorably to higher doses of vitamin C.

Practically, this research indicates that supplementing commercial channel catfish diets with higher than normal levels of vitamin C during early spring when the fish are most vulnerable to bacterial infections may be beneficial. Meyer (1970) reported that heaviest mortalities from bacterial infection in commercial catfish production occurred during the early spring season when water temperature was around 20°C. Because warmwater fish eat poorly during the winter, their body stores of ascorbic acid would likely be low at this time. Practical dietary levels of vitamin C should be 60 mg/kg for the summer growing season and at least 150 mg/kg for early spring feeding.

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Timing and Relative Intensity of Size-Selective Mortality of Juvenile Chum Salmon (*Oncorhynchus keta*) During Early Sea Life

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HEALEY, M. C. 1982. Timing and relative intensity of size-selective mortality of juvenile chum salmon (*Oncorhynchus keta*) during early sea life. Can. J. Fish. Aquat. Sci. 39: 952–957.

Available evidence indicates that mortality of juvenile salmon during early sea life is high and probably size dependent. I used scale analysis to determine the timing and relative intensity of size-selective mortality in chum salmon (*Oncorhynchus keta*) during early sea life. Significant size-selective mortality could be demonstrated only over the time period that the fish were laying down circuli 2–4 on their scales. The relative intensity of mortality for different sizes of fish suggested that mortality was strongly size selective over the size range 45–55 mm fork length. No particular mortality agent could be identified, but the size range involved corresponds with the size at which chum salmon move from very shallow water and nearshore habitat to open water pelagic habitat.

Key words: size-selective mortality, salmon, early sea life

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Les données disponibles révèlent que la mortalité des jeunes saumons au début de leur vie en mer est élevée et dépend probablement de leur longueur. J'ai analysé les écailles pour établir le moment et l'intensité relative de la mortalité reliée à la longueur chez le saumon kéta (*Oncorhynchus keta*) au début de la vie en mer. Une mortalité fortement reliée à la longueur ne pouvait être observée que pendant la période où le poisson déposait les anneaux de 2 à 4 ans sur ses écailles. L'intensité relative de la mortalité des différentes longueurs de poissons semble indiquer que la mortalité est fortement fonction de la longueur quand celle-ci dépasse la classe de 45 à 55 mm de longueur à la fourche. Aucun agent spécifique de mortalité n'a pu être identifié, mais la classe de longueur en cause correspond à la longueur que le saumon kéta a lorsqu'il quitte son habitat en eaux peu profondes et près des rivages pour se diriger vers un habitat dans les eaux pélagiques océaniques.

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MORTALITY of juvenile Pacific salmon during the first few weeks after they enter the sea is thought to be high and important in determining the number of returning adults (Parker 1962, 1968). Parker (1968) estimated that 55–77% of Bella Coola River pink salmon (*Oncorhynchus gorbuscha*) fry from 1961 to 1963 brood years failed to survive the first 40 d of ocean life. The rate of mortality during early sea life may be unique to each salmon stock, but within a stock, mortality appears to be related to the size and rate of growth of the fish; larger, faster-growing fish having the better survival (Parker 1962, 1971; Ricker 1962). Neither the timing of early ocean mortality nor the relative mortality of fish which are growing at different rates is well known.

Scale pattern is related to growth in salmonids. In particular, the spacing of circuli is positively correlated with growth and food supply (Bhatia 1931; Gray and Setna 1931; Bilton and Robins 1971a). The existence of this relationship offers a way to investigate size-selective mortality among juvenile salmon in the sea because, if the slower-growing members of a cohort are dying, their loss should result in wider average circulus spacing among the survivors. In this report I summarize information on circulus number and circulus spacing in young chum salmon (*O. keta*) and present evidence for size-selective mortality based on these measurements.

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Methods

If I am to demonstrate size-selective mortality by analysis of circulus spacing, the data must satisfy two conditions: circulus formation must be time dependent, and scale radius must be correlated with fish length. Circuli will then represent time checks on the scale, and their spacing will be positively correlated with rate of growth. Hence, if t d after emergence from the gravel the members of a cohort of chum fry have n circuli, then the larger members of the cohort will have more widely spaced circuli. Furthermore, after an additional number of days x during which mortality selective for smaller fish

occurs, the survivors of the cohort now aged $t + x$ will have wider average spacing of the first n circuli than that existing in the cohort at age t. Conversely, if mortality is selective for the larger fish, the survivors will have narrower average spacing of the first n circuli. The relative mortality of each size group in the population, represented by a particular circulus spacing, can be calculated by comparing the frequency distribution of circulus spacings at times t and $t + x$.

The condition that circulus formation must be time dependent will be met if there is a significant positive correlation between age and circulus count. The condition that scale radius must be correlated with fish length will be met if circulus spacing and fish length are positively correlated for fish of the same age. If these initial conditions are met, a significant correlation between circulus spacing and age will confirm the occurrence of size-selective mortality. For juvenile salmon, mortality is expected to be greater among the smaller fish so that the correlation between circulus spacing and age should be positive. Where these relationships occur, I can estimate the relative survival of different size classes by comparing the frequency of circulus spacings at two ages.

Chum salmon fry in southern British Columbia migrate to sea between March and May, accomplishing their downstream migration within a few days after emerging from the gravel redds. Migrant fry range 35–40 mm in length. Once in the sea they reside for a few weeks in shallow water near shore. During this period, although they grow rapidly, the fry are small (40–70 mm fork length) and presumably are vulnerable to various mortality agents. I investigated the dispersal and growth of chum salmon fry from the Nanaimo River on Vancouver Island, British Columbia, and their length of residence in various marine habitats near the river mouth in 1975 and 1976. In 1976 I collected scales for analysis. Information on other aspects of the study, of which the scale analysis was a part, and further details on methodology are presented elsewhere (Healey et al. 1977a, b; Healey 1979, 1980).

In 1976 I captured chum fry near the Nanaimo River mouth by inclined plane fry trap and marked them by spraying with fluorescent grit. I marked three different groups with different colors; red (April 7–19), green (April 20–May 2), and blue (May 3–24), and recaptured representatives of these groups within a 10-km radius of the river mouth between April 13 and June 16. The recaptures provided scales from juveniles of known age. "Age" was the time in days between the median day of release of the marked group and the day of recapture. I analyzed scales from 69 recaptures ranging in age from 5 to 50 d.

To estimate mortality of different size groups, I also analyzed scales from unmarked fry. To be comparable, samples must come from the same cohort of fry at different ages. This posed a significant problem in sampling unmarked fry. The knowledge obtained in 1975, that early marine growth was 1 mm per day and that fry tended to remain in the same location for several weeks, provided a method for sampling approximately the same cohort of fry at different ages in 1976 (Healey et al. 1977a, b). In May 1976, I took two samples of unmarked fry 20 d apart from near the Pacific Biological Station in Departure Bay, Vancouver Island. I selected fry from the first sample having scales with 4 or fewer circuli. These fish ranged 40–52 mm in fork length. At a growth rate

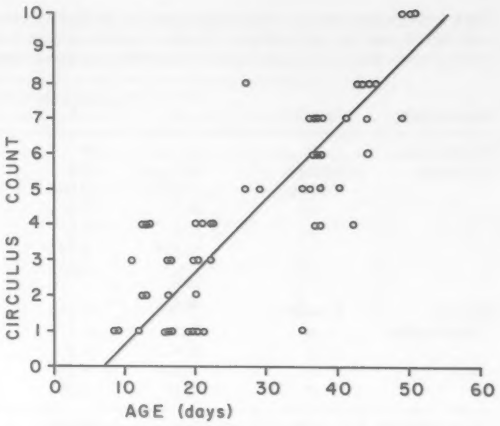

FIG. 1. The relationship between circulus count and age for marked fry from the Nanaimo River in 1976.

of 1.0 mm/d, fish which were 40–52 mm long in the first sample would be 60–72 mm long in the second sample. I selected fish of this size from the second sample and compared the circulus widths of their scales with those of fish from the first sample. Subsequent analysis showed that growth of fry marked in 1976 was again 1.0 mm/d, so that appropriate sizes of fry were selected for comparison in 1976.

I removed scales from the side of the fry between the dorsal fin and the lateral line by wiping the fish with a wire probe, and smeared these on a glass slide in a drop of water. I projected the smear on a piece of white paper at 45× magnification. I selected three clean and regularly shaped scales from each smear for measurement. For each scale I counted the circuli and measured the distance from the center of the focus to each circulus and to the margin of the scale along the anterior–posterior axis. Measurements from all three scales were averaged to give a single set of measurements for each fish.

Results

Thirteen of the 69 recaptures had no circuli on their scales. Circulus count was highly correlated with age among the remaining 56 marked fish whose scales had 1 or more circuli ($r = 0.826$, F test $P < 0.001$) (Fig. 1). The GM regression equation (Ricker 1973) of circulus count on age was:

$$\text{Count} = 0.208\ \text{Age} - 1.468.$$

There is considerable scatter in the relationship (Fig. 1), but a great deal of this may be due to the uncertainty in assigning age. Each group of fish was marked over a number of days, so that age at recapture could be under or overestimated by the difference between the median release date and the start or end of marking. This difference was 14 d for the 3rd marking period. Standard deviations around the median release dates were, however, much smaller, 3 d for red, 4 d for green, 5 d for blue, so that the assignment of age was more precise than

TABLE 1. Regression analysis of fish length (mm) on the distance (mm) between the last 2 circuli on the scale and the distance from the focus to the last circulus for fish having 1–7 circuli. Analysis includes both tagged and untagged fish.

Measurement	Statistic[a]	Number of circuli						
		1	2	3	4	5	6	7
Between last 2 circuli	N	22	64	99	26	41	26	20
	$\bar{x}$ length	42.5	45.5	48.8	54.7	62.7	67.0	71.6
	$\bar{x}$ width	0.092	0.048	0.044	0.042	0.040	0.040	0.038
	a	40.5	42.0	45.0	40.6	60.8	74.2	73.3
	b	21.4	73.6	88.0	333.3	47.0	−180.3	−43.4
	r	0.124	0.293	0.303	0.484	0.109	−0.299	−0.064
	P	>0.05	<0.025	<0.01	<0.025	>0.05	>0.05	>0.05
Focus to last circulus	$\bar{x}$ width	0.092	0.145	0.190	0.229	0.296	0.330	0.370
	a	40.5	41.5	37.6	12.5	40.9	63.4	50.7
	b	21.4	31.5	59.5	181.0	75.5	11.7	55.8
	r	0.124	0.171	0.432	0.782	0.528	0.077	0.363
	P	>0.05	>0.05	<0.01	<0.01	<0.01	>0.05	>0.05

[a] a = intercept, b = slope, r = correlation, P = probability.

TABLE 2. Regression analysis of circulus width on age; circulus width measured as the distance between circulus n and $n-1$, or distance between focus and circulus n. Analysis includes only tagged fish.

Measurement	Statistic	Circulus number					
		1	2	3	4	5	6
Between circulus "n" and "n−1"	N	50	50	46	40	30	22
	$\bar{x}$ age	32.2	32.2	33.6	36.0	40.1	42.0
	$\bar{x}$ width	0.092	0.051	0.049	0.046	0.041	0.041
	a	0.0080	0.0464	0.0336	0.0321	0.0316	0.0467
	b	0.000123	0.000153	0.000463	0.000385	0.000236	−0.000136
	r	0.180	0.220	0.517	0.452	0.185	−0.075
	P	>0.05	>0.05	<0.01	<0.01	>0.05	>0.05
Between focus and circulus "n"	$\bar{x}$ width	0.092	0.143	0.192	0.240	0.288	0.334
	a	0.0880	0.134	0.162	0.196	0.241	0.292
	b	0.000123	0.000279	0.000891	0.00123	0.00116	0.000961
	r	0.180	0.256	0.508	0.481	0.273	0.190
	P	>0.05	>0.05	<0.01	<0.01	>0.05	>0.05

the length of each marking period might imply. Assuming the regression equation describes the rate of circulus formation, then the 1st circulus was laid down, on average, after 12 d, and subsequent circuli were laid down every 5 d. The significant linear regression is taken to be adequate evidence that circulus formation was time dependent during the period under investigation.

The relationship between fry length and average circulus spacing among fry having the same number of circuli was investigated by correlating fry length with both the width of the last intercirculus space on the scale and with the distance from the center of the focus to the last circulus. The first comparison relates fry length to their most recent growth while the second relates length to growth since scale formation.

Fish length was significantly correlated with the width of the last intercirculus space among fish having 2, 3, or 4 circuli, but not among fish having 1, 5, 6, or 7 circuli (Table 1). As the fish get larger, presumably variation in length due to recent growth becomes masked by variation in length due to growth over the whole time since emergence. A weakening of the correlation between length and the width of the last intercirculus space is, therefore, to be expected. Sample size for scales with 5–7 circuli was also small. The absence of a correlation between fish length and the width from the center of the focus to the 1st circulus suggests that the size of the focus is independent of fish size.

The abrupt drop in the correlation coefficient between fish having 4 circuli and those having 5 circuli is inconsistent with the notion of a gradual weakening of the correlation between length and the width of the last intercirculus space as the fish get older. Small sample size and increasing variation among scales may be partly to blame. The regression slope increased up to the 4th circulus then dropped abruptly, however, and the slopes of the regressions for circuli 6 and 7 were negative, although not significant (Table 1). The abrupt changes in regression coefficients suggests that small sample size is not a sufficient explanation for the low correlation coefficient, and that some change in growth pattern may have occurred.

Fish length was significantly correlated with distance from the focus to the last circulus among fish with 3, 4, or 5 circuli, but not among fish with 1, 2, 6, or 7 circuli (Table 1). The

TABLE 3. Frequency of circulus width classes for circuli 0−1, 1−2, 2−3, 3−4 for samples of fry from the same cohort taken 20 d apart. χ^2 analysis is for the $r \times 2$ contingency table of circulus width frequencies with frequencies in the first two and last two width classes combined so that cell counts of <5 were mostly eliminated.

	Circulus measurement							
	0−1		1−2		2−3		3−4	
Circulus width, mm	Sample 1	Sample 2	Sample 1	Sample 2	Sample 1	Sample 2	Sample 1	Sample 2
0.03			5	2	7	2	5	3
0.04			43	19	47	17	8	22
0.05			60	31	24	37	2	41
0.06			30	35	16	29	1	19
0.07	5	1	2	1	0	3	0	3
0.08	24	9						
0.09	46	19						
0.10	59	50						
0.11	13	7						
0.12	6	2						
$\bar{x}$ width	0.0945	0.0967	0.0486	0.0516	0.0452	0.0516	0.0314	0.0497
χ^2	7.24		8.66		24.73		16.56	
df	3		2		2		1	
P	>0.05		<0.025		<0.001		<0.001	

TABLE 4. Percent frequency distributions for width classes of circuli 2−4 from samples taken 20 d apart (sample 1 and 2), relative rates of survival for each width class (from ratio B/A with B/A of width class 0.03 mm = 1.0), and fish length associated with each width class.

Circulus no.	Measurement category	Width class (mm)			
		0.03	0.04	0.05	≥0.06
1−2	Sample 1 % (A)	3.6	30.7	42.9	22.8
	Sample 2 % (B)	2.3	21.6	35.2	40.9
	B/A	0.64	0.70	0.82	1.79
	Relative survival	1.0	1.1	1.3	2.8
	Fish length	44.2	44.9	45.7	46.4
2−3	Sample 1 % (A)	7.4	50.0	25.5	17.0
	Sample 2 % (B)	2.3	19.3	42.0	36.4
	B/A	0.31	0.39	1.65	2.14
	Relative survival	1.0	1.2	5.3	6.9
	Fish length	47.6	48.5	49.4	50.3
3−4	Sample 1 % (A)	31.2	50.0	12.5	6.2
	Sample 2 % (B)	3.4	25.0	46.6	25.0
	B/A	0.11	0.50	3.78	4.03
	Relative survival	1.0	4.5	34.4	36.6
	Fish length	50.6	53.9	57.3	60.2

absence of a significant correlation among fish with 2 circuli was probably due to the relatively large variation in scale radius introduced by the focus. The failure to show significant correlation above 5 circuli, however, was unexpected. Among all the scales measured, fish length and scale radius were highly correlated ($r = 0.956$, $P < 0.001$). I expected that a significant correlation would be evident at all circulus counts even over the small range of lengths among fish having the same circulus count. The sample sizes in the 6 and 7 circulus groups were small; however, a significant correlation was evident among fish with 4 circuli for which the sample size was also small. Variation in both fish length and scale radius was about twice as great for fish with 4 circuli as it was for fish with 6 circuli, however, and this would make it more difficult to demonstrate significant correlation at the higher circulus count.

Apparently only circulus spacings up to the 5th circulus meet the criteria for demonstrating size-selective mortality. I regressed circulus width on age for circuli 1−6 to span the range of suitable circuli and to determine if a relationship between circulus spacing and age persisted beyond the range of suitable circuli. Such persistence might indicate spurious results. I used scales from marked fish having 2 or more circuli in the analysis, and used both the width between circuli

n and $n-1$ and the distance from the center of the focus to circulus n as dependent variables.

Although circuli 2–5 met the original criteria for detecting size-selective mortality, only measurements relating to circuli 3 and 4 were significantly correlated with age and thus demonstrated the existence of size-selective mortality (Table 2). Although significant, the regressions explained only 20–27% of the variation in circulus width.

I also compared width measurements for circuli 1–4 between the samples of unmarked fish captured 20 d apart in May 1976. In all instances the average distance between circuli was greater in the older fish (Table 3), and the relative difference increased with increasing circulus number. The difference between samples was significant ($P < 0.05$) for all but the 1st circulus (Table 3). These results corroborate the evidence from marked fish, that fish with wider circulus spacing (i.e. the larger fish) survived better. The larger sample of unmarked fish extends the evidence for size-selective mortality to fish having 2 circuli. The apparent increase in average circulus spacing over the 20 d in the unmarked sample was consistent with what would be expected from the regression slopes of circulus width on age for marked fish (Table 2).

I estimated the relative survival of fish of different sizes by converting the frequency distributions of circulus widths to proportional distributions, and calculating the ratio between samples of the proportions for each width class (Table 4). These ratios are proportional to the survival over 20 d of fish having the different circulus spacings. Because circulus spacing for circuli 2–4 is correlated with fish length (Table 1), I could calculate length classes represented by the circulus spacings (Table 4). The relative survival of the smallest (44.2 mm fork length) and largest (46.4 mm fork length) chum having 2 circuli was 1:2.8, whereas the relative survival of the smallest (50.6 mm) and largest (60.2 mm) chum having 4 circuli was 1:36.6 (Table 4). Thus, the intensity of size-selective mortality increased as the fish increased in size.

Among fish with 2 circuli, there was not much difference in relative survival of the three smallest size classes of fish, but survival increased twofold between the third largest and the largest size group. Among fish with 3 circuli, relative survival did not increase much between the two smallest size classes, jumped 4.4 times between the second and third size classes, then increased only slightly between the third and fourth size classes. Among fish having 4 circuli, relative survival increased 4.5 times between the first and second size classes, a further 7.5 times between the second and third size classes, then increased only slightly between the third and fourth size classes (Table 4). This pattern of relative mortality in relation to size suggests that the fish were growing through a size of particularly intense size-selective mortality.

Discussion

The existence of size-selective mortality among juvenile chum salmon is confirmed by the foregoing analysis of scale pattern. The necessary conditions for scale pattern to reflect size-selective mortality, positive correlations between age and circulus count and between circulus width and fish size, were met for circuli 2–5. Because of the strong correlation between age and circulus count ($r^2 = 0.682$), in spite of the uncertainty in age of recaptures, I suggest that circuli were laid down at fairly regular time intervals among these rapidly growing chum salmon. Numerous factors are known to influence the rate of circulus formation, however, and starved fish apparently do not lay down circuli (Bilton and Robins 1971a, b). The relationships observed in this study might, therefore, fail to apply to fish under a different feeding regime or over a wider range of individual growth rates.

Although fish length and circulus width were correlated among fish having 2–5 circuli, age and circulus width were correlated only for the 3rd and 4th circuli among marked fish and for the 2nd, 3rd, and 4th circuli for unmarked fish. This could be because the correlations between length and circulus spacing were relatively weak among fish with 2 and 5 circuli making it more difficult to demonstrate size-selective mortality from circulus spacing. Fish with 2 or 5 circuli met the criteria for demonstrating size-selective mortality by only one of the two circulus width measurements. An alternative hypothesis, however, is that mortality was strongly size selective only over a relatively small range of fish sizes. This hypothesis is consistent with a situation in which the young salmon grow through the size range available to a particular predator, as suggested by Parker (1971) and Sibert and Parker (1972) for coho salmon (*O. kisutch*) preying upon pink salmon fry.

The relative mortality rates of different size groups of fish are consistent with the hypothesis that mortality was strongly size selective over a limited range of fish sizes. The relative difference in survival among different sized fish having 2 circuli was only 3-fold, whereas it was 37-fold among fish having 4 circuli, indicating greatly increased size-selective mortality in the older fish. Furthermore, at 2 circuli only the largest fish had an advantage, while at 4 circuli only the smallest fish were at a disadvantage. Fish with 3 circuli were intermediate. Exactly this pattern would occur if the fish were outgrowing the ability of a particular predator to capture them. Considering the sizes of chum fry involved, mortality appears to be most strongly size selective over the size range 45–55 mm. This is the size range over which most chum fry leave very shallow nearshore habitat for more open pelagic habitat and could signify a change in potential predators (Healey 1980; Healey et al. 1977b).

Although these data appear to demonstrate strong size-selective mortality over a particular size range, this is not to imply that total mortality is greater over this size range. Mortality may well be greater where no size selection occurs. Nor can anything certain be said about the mechanism of size-selective mortality although predation seems the most likely.

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Life History Variations of Anadromous Cisco (*Coregonus artedii*), Lake Whitefish (*C. clupeaformis*), and Round Whitefish (*Prosopium cylindraceum*) Populations of Eastern James–Hudson Bay

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MORIN, R., J. J. DODSON, AND G. POWER. 1982. Life history variations of anadromous cisco (*Coregonus artedii*), lake whitefish (*C. clupeaformis*), and round whitefish (*Prosopium cylindraceum*) populations of eastern James–Hudson Bay. Can. J. Fish. Aquat. Sci. 39: 958–967.

Differences in life history among three species of anadromous coregonines from La Grande River, James Bay, were significant with lake whitefish (*Coregonus clupeaformis*) and round whitefish (*Prosopium cylindraceum*) displaying reproductive patterns more typical of harsh northern environments and characteristic of "K-selection," relative to cisco (*Coregonus artedii*). Interspecific differences at La Grande River were more apparent than intraspecific differences in life history traits of cisco and lake whitefish over the James–Hudson Bay range. Although cisco exhibit decreasing reproductive effort independent of growth over the North American range, thus conforming to life history theory, both growth and reproductive effort are reduced northwards over their James–Hudson Bay range. The observations suggest that physiological constraints related to the shorter growing season at the northern limit of cisco's coastal Hudson Bay range may overwhelm expected coadapted life history traits. Lake whitefish exhibit reduced reproductive effort independent of variations in growth northwards over their North American and James–Hudson Bay coastal range; this suggests coadaptation of life history traits that permit survival at northern sites.

Key words: reproduction, growth, life history theory, anadromous coregonines, James–Hudson Bay

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Il existe, parmi trois espèces de corégoninés anadromes de la Grande-Rivière (baie James), des différences significatives, le grand corégone (*Coregonus clupeaformis*) et le ménomini rond (*Prosopium cylindraceum*) montrant des modalités de reproduction plus typiques d'un environnement boréal rigoureux et caractéristiques d'une « sélection K », comparativement au cisco de lac (*Coregonus artedii*). Les différences interspécifiques observées à la Grande-Rivière sont plus prononcées que les différences intraspécifiques des caractéristiques du cycle biologique du cisco de lac et du grand corégone dans toute l'aire baie James–baie d'Hudson. Bien que le cisco de lac exhibe un effort reproducteur amoindri indépendant de la croissance dans son aire nord-américaine, en conformité avec la théorie du cycle biologique, la croissance et l'effort reproducteur sont tous deux diminués vers le nord dans le secteur baie James–baie d'Hudson. Ces observations donnent à penser que les

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contraintes physiologiques liées à une saison de croissance plus courte à la limite septentrionale de l'aire de distribution côtière du cisco de lac dans la baie d'Hudson peuvent supplanter les caractéristiques d'adaptation anticipées. Le grand corégone montre une reproduction diminuée indépendante des variations de la croissance, à mesure qu'on progresse vers le nord dans toute leur aire nord-américaine et dans le secteur côtier des baies James et d'Hudson; ceci laisse supposer une coadaptation des caractéristiques du cycle biologique favorisant la survie dans le nord.

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COMPARISONS of fish populations have indicated geographic differences in fecundity (Paulson and Smith 1977), egg size (Marshall 1953; Blaxter and Hempel 1963), and age of maturity (Nikolskii 1963). A general trend in northern fishes to reduce fecundity and increase the lifetime frequency of spawning has been noted by Nikolskii (1970) and Leggett and Carscadden (1978). Several hypotheses have been proposed to explain these observations. Ricker (1954), Murphy (1966), Schaffer (1974), Schaffer and Elson (1975), and Leggett and Carscadden (1978) provided evidence for the selection of repeated spawning, late maturity, and decreased annual fecundity in fish inhabiting unstable environments as a means of reducing the probability of extinction in the face of wide fluctuations in juvenile mortality. Cody (1966), Holgate (1967), Gadgil and Bossert (1970), Charnov and Krebs (1973), and Mountford (1973) have variously hypothesized that there may be a trade-off in energy allocation among growth, maintenance, and reproduction that maximizes the individual's contribution to future genotypes. In the harsher, shorter, growing season of the north, reduced fecundity may be an adaptation to ensure an adequate allocation of energy from a restricted energy budget to maintenance and growth. Reduced fecundity may be balanced by increased longevity permitting more potential maturation cycles.

Evolutionary interpretations of observed life history variations, while conceptually appealing, are not uniformly held. Nikolskii (1969) and Bagenal (1978) have cautioned against assuming adaptive significance in life history variations within species in view of the effects of such proximate factors as temperature, light, and food on growth, fecundity, and maturity of fish. Stearns (1977) implies that there is little point in trying to match empirical results to current theories because they are based on such oversimplified assumptions and ambiguities, that contrasting models based on different assumptions produce similar predictions. In a subsequent paper (Stearns 1980), he suggests that life history tactics per se may be intrinsically organized in such a way that they do not respond similarly to selection and as a consequence, the direction of response to a particular set of conditions may not be predictable.

This paper describes the way in which anadromous stocks of cisco (*Coregonus artedii*), lake whitefish (*C. clupeaformis*), and round whitefish (*Prosopium cylindraceum*), occurring along 900 km of the eastern James–Hudson Bay coast, vary in life history. These populations, although subject to some exploitation by native subsistence fisheries (Berkes 1982), are believed to be in stable equilibrium with their physical and biotic environment. They thus provide an opportunity to verify whether shifts in life history traits along a south–north gradient conform to the pattern generally observed and typed "K-selection": increased ages at maturity, fewer but larger young, a longer life expectancy, and smaller reproductive efforts.

This is the first synthesis of information on the biology of the anadromous stocks of whitefish in James–Hudson Bay. These stocks have assumed considerable importance in recent years because of the potential impacts of hydroelectric developments in progress or planned along this coast. The James Bay and Northern Quebec Agreement (1976), Section 24, provides for guaranteed levels of harvest of these species by native fishermen, where stocks permit. Published information on the present status of the stocks will be important when decisions have to be made on the management of native fisheries as conditions along the coast are modified by man.

Materials and Methods

STUDY AREA AND CLIMATE

Cisco, lake whitefish, and round whitefish were collected from the lower portions and estuaries of rivers and in bays along the east coast of James–Hudson Bay (Fig. 1, Table 1). The species are associated with freshwater discharges into the Bay and return to freshwater for reproduction and overwintering (Morin et al. 1981).

The climate of Hudson Bay is arctic; James Bay is milder, but its mean annual temperature is less than most of Canada at similar latitudes (Thompson 1968). The coastlines have continental, rather than maritime, climates as a result of extensive ice cover over several months. There are wide extremes of temperature between winter and summer. The growing season (mean daily temperature >5.6°C) ranges from 140 d at Rupert's Bay to 80 d at Innuksuac River (Wilson 1971). The effects upon terrestrial vegetation are evident in the transition from boreal forest along the coast of James Bay and southern Hudson Bay to tundra to the north of Richmond Gulf. The coast is cool during spring and summer, especially in the north, as prevailing winds cross the ice-packed bay and extensive fog banks form along the coastal hills. James and Hudson bays are usually clear of ice from late August until late October (El-Sabh and Koutitonsky 1977; Larnder 1968).

SAMPLING

Most fish collections were made by gillnetting. The most frequently used gill nets measured 45.7 × 1.8 m and were formed of six panels of multifilament mesh graded 25, 38, 51, 64, 76, and 102 mm (stretched measure). Collections made in Richmond Gulf, Eastmain River, and in the upper La Grande

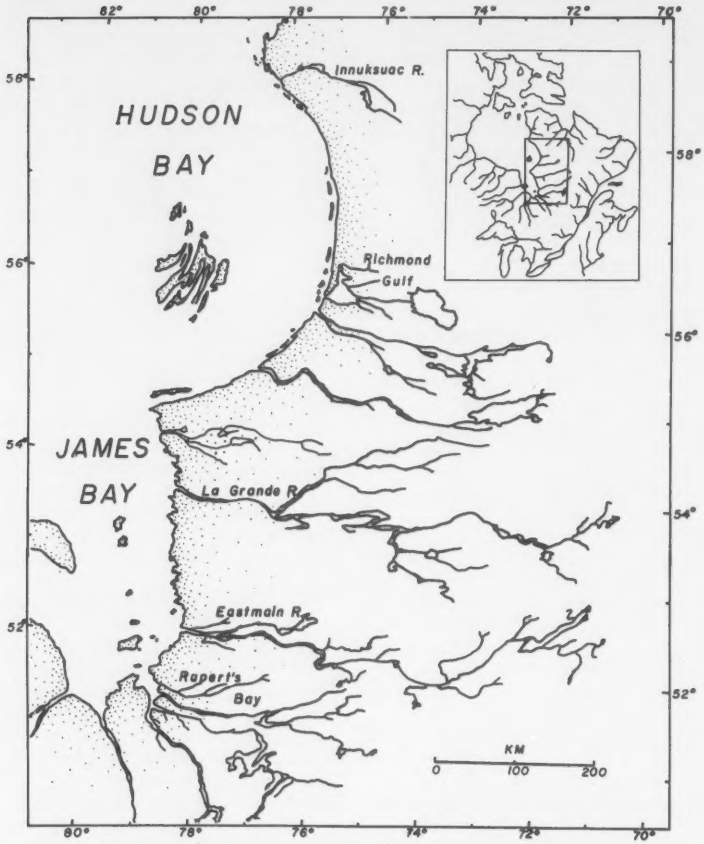

FIG. 1. East coast of James and Hudson bays, indicating the rivers and estuaries studied.

TABLE 1. The major physical characteristics of the rivers studied. Data for Rupert's Bay includes the Nottaway, Broadback, and Rupert rivers. Data for Richmond Gulf is based on measures of the l'Eau-Claire River. Mean breakup date is taken from Wilson (1971).

River	Latitude	Drainage area ($km^2 \times 1000$)	Mean annual flow ($m^3 s^{-1}$)	Mean date of breakup
Rupert's	51°40′	138.0	2549	May 1
Eastmain	52°15′	46.4	603	May 10
La Grande	53°50′	97.6	1700	May 20
Richmond Gulf	56°15′	4.5	86	June 1
Innuksuac	58°26′	11.4	101	June 20

River also included single-meshed gill nets of mesh sizes 38, 51, 64, 89, and 102 mm. Seining was conducted at the rapids of La Grande River for cisco and lake whitefish using the method described by Berkes (1976).

The Eastmain and La Grande rivers, and Richmond Gulf, were sampled from 1973 to 1975. Age, growth, and fecundity analyses for these three sites were based on 1974 data, while analyses of age at maturity and egg size were made by combining data for all years. The growth and age structure of spawning coregonines in La Grande River are from samples taken at the La Grande River rapids in 1973. Rupert's Bay and the Innuksuac River were sampled in 1976 and 1977, respectively.

LIFE HISTORY VARIABLES

Age was determined from two independent readings for each specimen using scales and/or otoliths for fish aged 1+

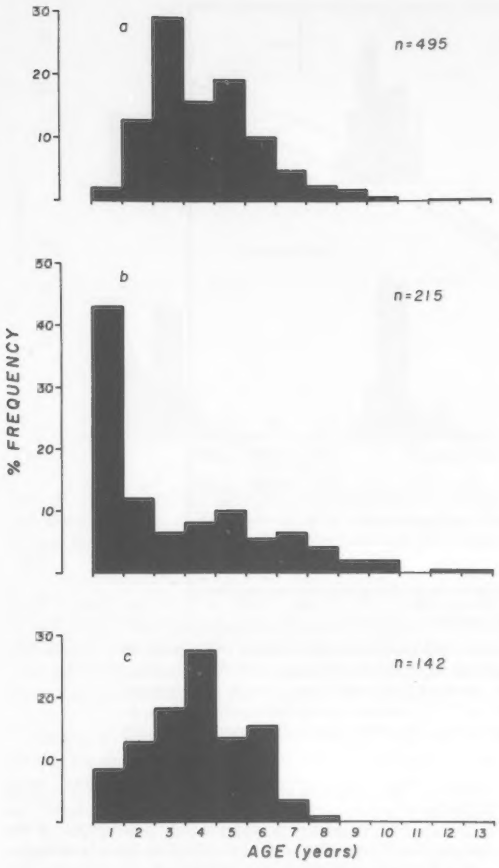

FIG. 2. Age-frequency distributions of (a) cisco, (b) lake whitefish, and (c) round whitefish captured in the lower La Grande River and estuary from July to October 1974.

to 8+ and sectioned otoliths for fish older than 8+. In case of disagreement between the first two readings a third reading was made to determine the age. All whitefish from Richmond Gulf and lake whitefish from the upper La Grande River were aged by scales alone. Age determination of lake whitefish by the scale method frequently underestimates the age of older specimens when compared with the corresponding age determined from otoliths (Power 1978). In the present study, comparisons of age determined by scales and by otoliths indicated that the scales of cisco and round whitefish may underestimate age by as much as 16 yr above a scale age of 8 yr. Caution must be exercised, therefore, in interpreting growth and population structure beyond the 8th year-class where scales only were used.

Back-calculated fork lengths at each scale annulus were fitted to a von Bertalanffy growth model (Abramson 1965) for cisco and lake whitefish of the La Grande River estuary. These data were examined for the presence of Lee's phenomenon which might indicate that growth curves were biased by size-selective mortality or by sampling bias (Ricker 1969). Lee's phenomenon was not detected in either the cisco or lake whitefish population of the lower La Grande River. Magnin and Clément (1979) fitted the same model to the back-calculated lengths of round whitefish in the lower La Grande River, and their pertinent results are presented.

Interpopulation comparisons of growth were made by comparing the observed fork lengths at each age-class over the range of estuaries sampled. This procedure was adopted to allow accurate comparisons of growth between young actively growing age-classes and to avoid possible errors from inaccurate age determination using scales for older fish. The Student–Newman–Keuls test (Sokal and Rohlf 1969) was used to test the significance of the differences between mean fork lengths.

All specimens captured were sexed and a descriptive evaluation of the stage of maturity was made. No reliable identification could be made of fish which had never previously spawned; however, maturing fish could be readily identified by mid-July using the criteria outlined by Nikolskii (1963). The complete ovaries of mature females sampled in the Eastmain, La Grande, and Innuksuac rivers and Richmond Gulf were preserved in 10% formalin. In the laboratory, the ovaries were weighed to the nearest 0.1 g and rinsed and kneaded to separate the ovarian tissue. Egg diameter was measured taking the mean of four measurements of 10 eggs aligned on a millimetre ruler. Eggs were counted in a subsample of 25 to 30% (up to 5000 eggs), of each set of ovaries. The subsample and the balance of the ovaries were air-dried to a constant weight, then weighed to the nearest milligram, and the number of eggs determined by direct proportion. The comparison of this method with whole counts was made on four specimens, and the difference varied between −0.6 and 1.1%. Healey and Nicol (1975), using similar methods, reported an error of ±2%.

Fecundity was regressed on net body weight (whole body weight minus weight of ovaries), and regression lines were compared by analysis of covariance (Snedecor and Cochran 1967). To evaluate the egg size of each species at similar stages of maturity, mean egg diameter was regressed on gonadosomatic index (GSI) and the regression lines compared by analysis of covariance. The gonadosomatic index, determined by dividing the weight of gonads by the total body weight of the fish, also provided a measure of sexual maturity.

The growth and reproductive characteristics of cisco and lake and round whitefish were first compared for La Grande River. La Grande River was chosen because it is located near the middle of the coastal range of sample sites and because the three species cohabit there. Secondly when possible, the same characteristics were compared separately for cisco and lake whitefish among sample sites along the coast. Data on the growth and reproduction of round whitefish were insufficient for a similar analysis of interpopulation variation.

Results

INTERSPECIFIC COMPARISONS — LA GRANDE RIVER

Age frequency — Age-frequency distributions of whitefishes sampled in La Grande River (Fig. 2) show that lon-

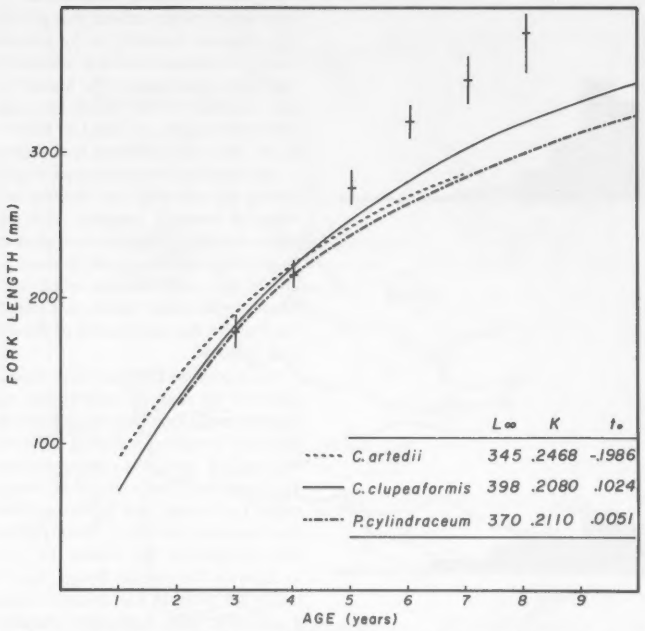

FIG. 3. Back-calculated growth of cisco, lake whitefish, and round whitefish captured in the lower La Grande River and estuary. Horizontal and vertical bars indicate the mean fork lengths and 95% confidence limits, respectively, of lake whitefish captured at the rapids of La Grande River. Curves were modeled according to the von Bertalanffy equation $L_t = L_\infty [1 - e^{-k(t-t_0)}]$, where L_t is the fork length at year t; L_∞ is the asymptotic fork length; k is a growth coefficient; and t_0 is the time when length would theoretically equal zero.

TABLE 2. Regressions of the logarithm of fecundity (y) on the logarithm of net body weight (x) for cisco, lake whitefish, and round whitefish from La Grande River. n = number of fish sampled; r = correlation coefficient obtained for the two variables x and y; P = probability level of significance of r.

Species	Regression equation	n	r	P
Cisco	$y=2.550+0.562x$	25	0.74	<0.01
Lake whitefish	$y=1.973+0.787x$	20	0.79	<0.01
Round whitefish	$y=1.179+0.934x$	18	0.73	<0.01

TABLE 3. Regressions of the logarithm of egg diameter (y) on the logarithm of gonadosomatic index (x) for cisco, lake whitefish, and round whitefish from the La Grande River. n = number of fish sampled; r = correlation coefficient obtained for the two variables x and y; P = probability level of significance of r.

Species	Regression equation	n	r	P
Cisco	$y=0.912+0.280x$	41	0.86	<0.01
Lake whitefish	$y=0.737+0.410x$	20	0.84	<0.01
Round whitefish	$y=0.168+0.232x$	17	0.70	<0.01

gevity is potentially greatest for lake whitefish followed by cisco and round whitefish. The maximum ages and corresponding fork lengths found over the entire 3-yr sampling period were for lake whitefish 17+ (446 mm), for cisco 13+ (367 mm), and for round whitefish 12+ (390 mm, Magnin and Clément 1979).

Growth — Back-calculated growth curves of the three species in the lower La Grande River and estuary indicate that cisco attain a slightly larger body size in their early years than either round or lake whitefish (Fig. 3). Growth of cisco subsequently diminishes and they reach the smallest asymptotic length.

The von Bertalanffy model of growth calculated for lake whitefish (Fig. 3) captured in the lower La Grande River and estuary predicted an asymptotic fork length (389 mm) much smaller than the fork lengths commonly found in the river system. An analysis of the migrations of anadromous coregonines in La Grande River (Morin et al. 1981) indicated that lake whitefish collections at the river mouth were predominantly of small and juvenile fish with larger and more mature individuals migrating directly to the first rapids of La Grande River for the autumn spawning period. Migrating lake whitefish were not captured by gill nets at the river mouth. A comparison of the back-calculated lengths of lake whitefish captured at the rapids and at the river mouth (Fig. 3) revealed no significant differences for 3- and 4-yr-olds (t-test $P > 0.05$ for both ages). However, the mean fork lengths of 5- to 8-yr-olds captured at the rapids were significantly greater than the same age-groups captured at the mouth of the river (age

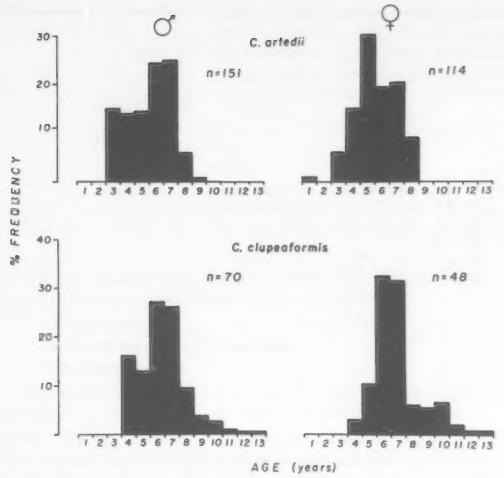

FIG. 4. Age-frequency distributions of spawning cisco (*C. artedii*) and lake whitefish (*C. clupeaformis*) captured at the first rapids of La Grande River, located 37 km upriver, during September and October 1973.

5: $P < 0.05$; age 6: $P < 0.001$; age 7: $P < 0.001$; age 8: $P < 0.001$). Therefore, samples of lake whitefish collected at the mouth of the river were biased towards smaller fish, also lake whitefish achieved the greatest asymptotic length of the three species, probably in the range of 450–500 mm.

Fecundity — No significant difference was observed among the slopes of the regressions of log fecundity on log net body weight in cisco, lake whitefish, and round whitefish (Table 2; analysis of covariance $P > 0.05$). The adjusted mean fecundities of cisco and lake whitefish did not differ significantly ($P > 0.05$), but were both significantly greater than that of round whitefish ($P < 0.001$).

Egg size — No significant differences were found among the slopes of the regression lines of log egg diameter on log gonadosomatic index (GSI) in cisco, lake whitefish, and round whitefish whereas differences between mean egg diameters were highly significant for each set of regressions tested (Table 3; analysis of covariance $P < 0.001$ in each comparison). For equivalent values of GSI, the egg diameter of round whitefish was greatest, that of cisco smallest, and lake whitefish intermediate.

Age at maturity — The ages of spawning cisco and lake whitefish populations, determined from samples taken at the rapids of La Grande River during September and October 1973 (Fig. 4), indicate that cisco mature earlier than lake whitefish. The most abundant age-group for female cisco was 5+, while 6+ and 7+ yr-old females were commonest among the lake whitefish. The most abundant age-classes of mature males for both species were 6+ and 7+ yr-olds. Similar data were unavailable for round whitefish.

In northern fish populations that do not spawn yearly, there is no simple criterion for identifying the age at maturity. There

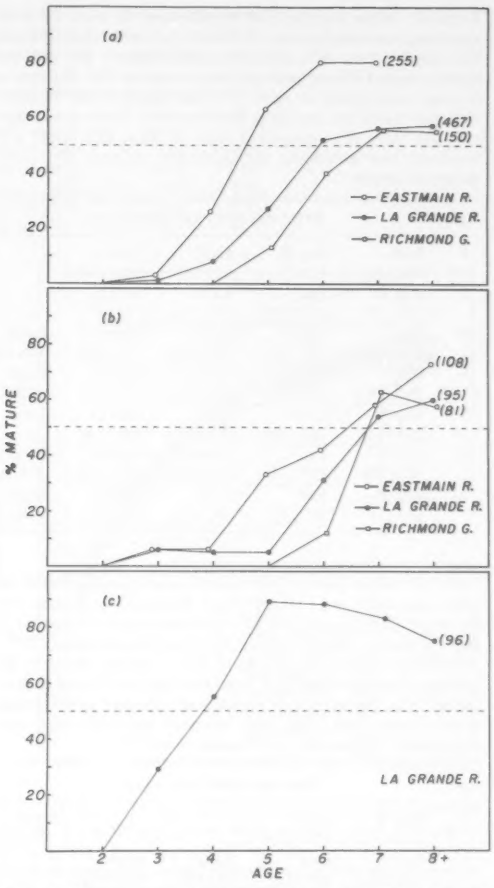

FIG. 5. Percent mature females in each age-class of (a) cisco, (b) lake whitefish, and (c) round whitefish from indicated sites along eastern James–Hudson Bay in 1974. Broken lines indicate the 50% mature level. Numbers in parentheses represent number of fish analyzed from each site.

is normally an increase in the percentage of maturing fish with age which peaks at an age and level set by the frequency of spawning, the age of first maturity, and the pattern of mortality. In this study, the youngest age-group in which at least 50% of the fish were maturing to spawn was adopted as the age of maturity. In La Grande River, round whitefish matured at age 4+, cisco at age 6+, and lake whitefish at age 7+ (Fig. 5).

INTRASPECIFIC COMPARISONS

The growth of cisco declined towards the north of their James–Hudson Bay range. The results of the Student–Newman–Keuls test applied to the observed mean fork lengths of cisco aged 1+ to 7+ (Table 4) indicated that the growth of cisco was significantly less in the Richmond Gulf

TABLE 4. Mean observed fork lengths (mm) of cisco for given age-classes and sampled rivers. Eastmain, La Grande, and Richmond Gulf data are from 1974 summer samples. Rupert's Bay data was taken in spring 1976 and Innuksuac data in summer 1977. Differences in mean fork lengths of ages 1–7 were tested by the Student–Newman–Keuls test, excluding Innuksuac data. Rivers in each age-class are arranged in descending order of mean fork length with horizontal bars underlining nonsignificantly different ($P > 0.05$) mean fork lengths.

Age	River and mean fork length (n)				
1	East	Rup B	La G	Rich G	
	130 (14)	126 (7)	121 (5)	102 (244)	
2	Rup B	East	La G	Rich G	
	190 (17)	187 (175)	186 (33)	175 (8)	
3	East	Rup B	La G	Rich G	Innuk
	241 (205)	231 (30)	227 (75)	195 (58)	196 (3)
4	East	Rup B	La G	Rich G	Innuk
	265 (137)	262 (15)	260 (43)	242 (41)	217 (2)
5	Rup B	East	La G	Rich G	Innuk
	288 (14)	285 (120)	276 (38)	267 (74)	241 (1)
6	Rup B	East	Rich G	La G	Innuk
	310 (10)	297 (74)	294 (47)	292 (17)	273 (1)
7	Rup B	East	La G	Rich G	Innuk
	343 (1)	305 (15)	301 (15)	300 (65)	244 (1)

TABLE 5. Mean observed fork lengths (mm) of lake whitefish for given age-classes and sampled rivers. Eastmain, La Grande, and Richmond Gulf data are from 1974 summer samples. Rupert's Bay data was taken in spring 1976 and Innuksuac data in summer 1977. Differences in mean fork lengths of ages 1–8 were tested by the Student–Newman–Keuls test. Innuksuac data were tested for age-classes 2–4. Rivers in each age-class are arranged in descending order of mean fork length with horizontal bars underlining non-significantly different ($P > 0.05$) mean fork lengths.

Age	River and mean fork length (n)				
1	Rup B	La G			Innuk
	126 (13)	121 (100)			122 (1)
2	Rup B	East	La G	Innuk	
	188 (8)	188 (61)	183 (33)	183 (16)	
3	Rup B	Innuk	Rich G	La G	East
	248 (16)	242 (29)	237 (34)	220 (27)	215 (95)
4	Innuk	Rup B	Rich G	La G	East
	304 (38)	285 (13)	260 (14)	257 (27)	257 (21)
5	Rich G	Rup B	La G	East	Innuk
	334 (6)	318 (10)	299 (12)	295 (13)	321 (2)
6	Rich G	Rup B	East	La G	Innuk
	330 (22)	327 (15)	323 (20)	278 (9)	334 (1)
7	Rich G	Rup B	East	La G	Innuk
	375 (12)	347 (11)	337 (46)	323 (17)	421 (1)
8	Rup B	La G	East	Rich G	Innuk
	375 (4)	363 (10)	362 (20)	362 (21)	361 (1)

population over four of the first five year-classes. Limited data presented for the Innuksuac River population (Table 4) suggest that the growth of cisco is further reduced in estuaries north of Richmond Gulf.

The growth of lake whitefish differed significantly in five of the eight year-classes tested over a range of sites (Table 5), but this variation could not be attributed to a latitudinal cline. Over all ages tested, the growth of lake whitefish in Rupert's Bay was similar to growth in Richmond Gulf or Innuksuac populations.

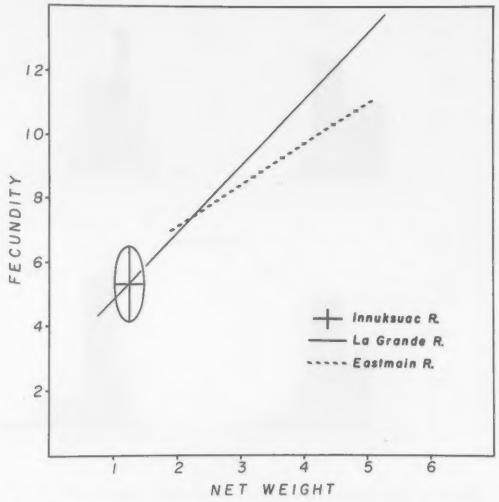

FIG. 6. Comparisons of fecundity (in units of 1000 eggs) net body weight (in units of 100 g) relations for different populations of cisco located along coastal James–Hudson Bay. The mean net weight and mean fecundity of Innuksuac River cisco are indicated by the intersection of horizontal and vertical bars, which also indicate the 95% confidence limits of net weight and fecundity.

Female cisco attained 50% maturity at the age of 5+ in the Eastmain River, 6+ in La Grande River, and 7+ in Richmond Gulf indicating increased age of maturity with increasing latitude (Fig. 5). Furthermore, the more northerly cisco skip reproduction more frequently as there were lower percentages of maturing female cisco in the older age-groups from La Grande River and Richmond Gulf than from the Eastmain River.

The age of 50% maturity for female lake whitefish remained at age 7+ in all populations examined (Fig. 5), and percent maturity in the older age-groups remained more or less constant for all three populations. There were, however, more young mature females in the Eastmain population and fewer northwards.

Cisco show no evidence of latitudinal variation in fecundity along the James–Hudson Bay coast. Analysis of covariance indicated no significant difference ($P > 0.05$) between the slopes or elevations of fecundity on length for cisco from Eastmain and La Grande rivers (slopes: df = 1,32; F = 1,319; means: df = 1,33; F = 0.567) (Table 6) (Fig. 6). No apparent difference in fecundity can be seen between the Innuksuac sample and the Eastmain and La Grande River samples.

Fecundity of lake whitefish was lower in Richmond Gulf than in La Grande River which may reflect a northward decline in fecundity (analysis of covariance $P < 0.005$) (Table 6).

Because of heteroscedacity in egg diameter data, the analysis of intraspecific variations in the egg size of cisco and lake whitefish by regression of egg diameter on GSI could not be

TABLE 6. Regressions of the logarithm of fecundity (y) on the logarithm of net body weight (x) for several James–Hudson Bay whitefish stocks. n = number of fish sampled; r = correlation coefficient obtained for the two variables x and y; P = probability level of significance of r.

Species	Location	Equation	n	r	P
Cisco	Eastmain	$y=4528.7+12.9x$	11	0.60	<0.05
Cisco	La Grande	$y=2709.7+20.9x$	25	0.84	<0.01
Lake whitefish	Richmond Gulf	$y=491.6+18.9x$	23	0.91	<0.01
Lake whitefish	La Grande	$y=357.5+22.9x$	20	0.92	<0.01

carried out. Qualitatively speaking, no obvious differences in egg size between populations were evident.

Discussion

Interspecific comparisons of the life history traits of anadromous cisco and lake and round whitefish of La Grande River indicate patterns that generally conform to the predictions of life history theory when considered in relation to observed patterns of species dominance along James–Hudson bay. Round whitefish exhibit a "K-selected" pattern of reproductive traits, with notably lower fecundity and larger egg size than cisco or lake whitefish. Round whitefish are more northern in distribution, being present in northern estuaries of James–Hudson Bay, but absent from estuaries of southern James Bay (Morin et al. 1980). In contrast, cisco dominate estuarine species assemblages in southern James Bay, but attain the limit of their distribution in northern Hudson Bay.

Intraspecific comparisons of the life history traits of anadromous cisco and lake whitefish along the James–Hudson Bay coast do not clearly conform to the pattern typed "K-selection." This would predict reduced fecundity, increased age at maturity, and more iteroparity northwards. Our data show that cisco grow more slowly (Table 4), mature older (Fig. 5), but do not exhibit reductions in fecundity (Table 6, Fig. 6) with increasing latitude. Limited evidence suggests that fecundity of lake whitefish diminishes northwards independent of variations in growth whereas age at maturity remains constant along the coast. These ambiguous patterns of reproductive traits may be due to physiological constraints overwhelming expected patterns of coadapted traits, as suggested by Stearns (1980), or be due to comparisons being made over too small a range of environmental conditions so that local variations confuse the general trends. To evaluate these possibilities, the following discussion deals with evidence for the selection of reduced reproductive effort independent of variations in growth within cisco and lake whitefish populations northwards over their North American range and compares such trends with patterns observed over the more-restricted James–Hudson Bay range.

Intraspecific comparisons of the growth and reproductive effort of cisco over their North American range reveal a pattern of decreased fecundity and delayed maturity northwards independent of variations in growth which conforms to the predictions of live history theory. Cisco fecundities decline towards the north of their range (Fig. 7), although limited data are available. Female cisco tend to mature later towards the north of their range, maturing at 1 and 2 yr of age in Clear Lake and Trout Lake (Hile 1936); at age 5 in Lake Ontario (Stone 1938); and at age 6 in La Grande River.

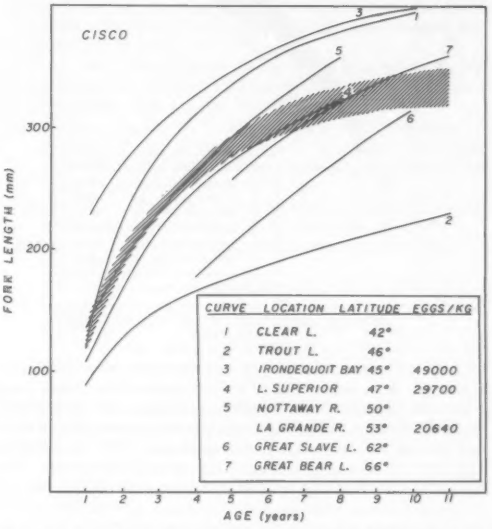

FIG. 7. Growth and fecundity of cisco at various latitudes in North America. Fecundity is expressed as the number of eggs produced by a 1-kg female. The hatched band indicates the range of observed growth of cisco along coastal James Bay. The fecundity of cisco in La Grande River is based on the relation: eggs = 2530.2 + 18.1 body weight (n = 25, r = 0.88, $P < 0.01$). Data sources are as follows: curves 1 and 2 — Hile (1936); curve 3 — Stone (1938); curve 4 — Dryer and Beil (1964); curve 5 — Magnin (1977); curve 6 — Bond and Turnbull (1973); curve 7 — Kennedy (1949). All curves were fitted by eye to mean fork length data.

The growth of James Bay cisco is the same as that of non-anadromous populations at similar latitudes and not appreciably greater or less than more northerly or southerly populations, respectively (Fig. 7). Hile (1936) illustrated the importance of the interactions of biotic and abiotic factors in contributing to the widely varying growth rates of cisco in four Wisconsin lakes (Fig. 7). The growth rate in each lake was related to the length of the growing season and inversely related to the density of cisco in each lake. According to scale analysis, cisco grew during a period of over 5 mo in Clear Lake and 3 mo in Trout Lake. The reduced growing period in Trout Lake was attributed to less food availability and earlier gonad development, factors that might also be related to the

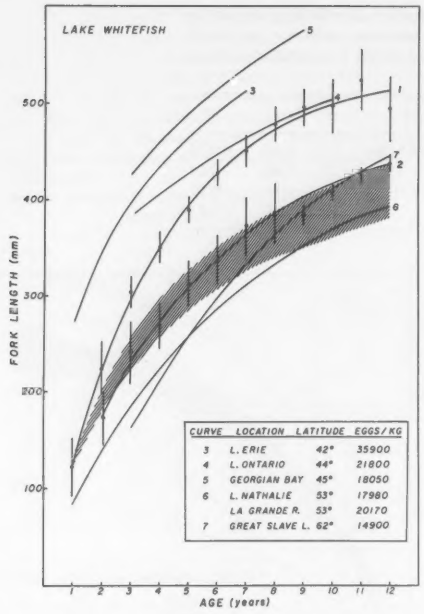
LAKE WHITEFISH
FORK LENGTH (mm)
AGE (years)
CURVE LOCATION LATITUDE EGGS/KG
3 L. ERIE 42° 35900
4 L. ONTARIO 44° 21800
5 GEORGIAN BAY 45° 18050
6 L. NATHALIE 53° 17980
LA GRANDE R. 53° 20170
7 GREAT SLAVE L. 62° 14900

FIG. 8. Growth and fecundity of lake whitefish at various latitudes in North America and at different levels of exploitation. Curves 1 and 2 show the growth of lake whitefish at medium and low levels of exploitation, respectively, with mean fork length and standard error indicated for each year-class (based on Healey 1975). Fecundity is expressed as the number of eggs produced by a 1-kg female. The hatched band indicates the range of observed growth of lake whitefish along coastal James–Hudson Bay. The fecundity of lake whitefish in La Grande River is based on the relation: eggs = 170.4 + 20.0 body weight ($n = 20$, $r = 0.92$, $P < 0.001$). Data sources are as follows: curve 3 — Van Oosten and Hile (1947), (fecundity — Lawler 1961); curve 4 — Hart (1931); curve 5 — Cucin and Regier (1966); curve 6 — Dumont and Fortin (1978); curve 7 — Kennedy (1953). All curves were fitted by eye to mean fork length data.

higher density of cisco in Trout Lake. The anadromous cisco of James Bay have an approximate 4-mo growing period in estuarine and nearshore feeding conditions, and density effects such as found in lake populations probably do not operate in this environment.

The cisco populations of James–Hudson Bay do not exhibit the expected pattern of reduced reproductive effort independent of variations in growth with increasing latitude observed over their North American range. As cisco reach the northern limit of their coastal range in Hudson Bay (Morin et al. 1980), reduced growth may be due to colder temperatures and shorter growing seasons. The later maturity observed may result from reduced growth while the fecundity of cisco, which remains unchanged along the coast, may already be minimal. The observation that the more northerly cisco skip reproduction more frequently than the Eastmain population represents one way in which reproductive effort can be reduced beyond a minimal fecundity. Therefore, these changes along the James–Hudson Bay coast may not represent adaptive strategies, but responses to temperature stress whereby further trade-offs in energy allocation between reproduction and growth is physiologically not possible.

Intraspecific comparisons of the reproductive effort of lake whitefish over their North American range reveals a pattern of decreased fecundity and delayed maturity with increasing latitude and conforms to the pattern predicted by life history theory. Lake whitefish fecundities generally decline towards the north of their range (Fig. 8). Female lake whitefish tend to mature later towards the north of their range, maturing at age 4 in lake Erie (Lawler 1961), at age 5 in Georgian Bay (Cucin and Regier 1966), at age 7 in La Grande River, and at age 8 in Great Slave lake (Kennedy 1953).

The relationship between lake whitefish growth, fecundity, and latitude is ambiguous and confounded by the effects of exploitation. Healey (1975) reviewed the data on lake whitefish growth and found that growth in unexploited populations was inferior at the northern and southern limits of its range, with best growth occurring in regions with 890–1200 degree days above 5.6°C. Air temperatures along the eastern coast of James–Hudson Bay are below the optimal temperature range with 890 degree-days above 5.6°C at Rupert's Bay decreasing to 330 degree-days above 5.6°C at the Innuksuac river (Wilson 1971). Growth, however, is positively affected by exploitation (Healey 1975, 1980), and James–Hudson Bay lake whitefish exhibit growth similar to that in lake populations at low levels of exploitation and greater than that in unexploited lake populations at similar latitudes. Healey (1978) reported that increased fecundity in lake whitefish populations following exploitation was not apparently related to more rapid growth.

The lake whitefish populations of James–Hudson Bay exhibit reduced fecundity northwards independent of variations in growth, and this conforms to the pattern predicted by life history theory. These observations may constitute limited evidence for an adaptive strategy. This conclusion is supported by the observation that lake whitefish maintain their abundance along the coast of Hudson Bay (Morin et al. 1980).

In conclusion, predictions based on life history theory could not be consistently satisfied by the comparison of life history traits at the species and population levels. Interspecific comparisons generally conformed to predictions when considered in relation to observed patterns of coregonine species dominance along James–Hudson Bay. Intraspecific comparisons, while conforming to the predictions of life history theory over the North American range of cisco and lake whitefish, revealed only weak evidence for adaptiveness along James–Hudson Bay and more likely represent the physiological consequences of harsher climatic conditions at northern sites of James–Hudson Bay.

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Trophic Structure, Reproductive Success, and Growth Rate of Fishes in a Natural and Modified Headwater Stream

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The impact of removing riparian vegetation, channel straightening, and fluctuations in flow regime on trophic structure, reproductive success, and growth rate of fishes was assessed in a natural (Jordan Creek (JC)) and modified (Big Ditch (BD)) headwater stream in east-central Illinois. Shallow habitats and organic substrates increased more in BD than JC during low flow periods in summer. Insect densities in JC were highest in late spring, declining to low levels by late summer. Insect densities in BD were high throughout summer. Fish in JC were predominantly benthic insectivores and insectivore–piscivores; trophic structure, age structure, and biomass were stable between years and seasons; recruits made up a small and stable portion of community biomass and were primarily insectivore–piscivores and generalized insectivores; younger age-classes were in shallow riffle habitats. Adult fish and recruits in BD were predominantly generalized insectivores, omnivores, and herbivore–detritivores; the last two were primarily mid-river species (*Carpoides cyprinus* and *Dorosoma cepedianum*). Considerable seasonal and annual variation in trophic structure, total biomass, and age structure occurred in BD associated with annual fluctuations in flow regime, abundance of organic substrates, and reproductive success of mid-river species. Younger age-classes had higher summer growth rates in BD than JC. The temporally variable physical environment and unstable autotrophic energy base created in modified headwater streams are probably major factors responsible for recent shifts in large river fish communities in the midwestern United States from insectivore and insectivore–piscivore species to omnivores and herbivore–detritivores.

Key words: community organization, fishes, Illinois, stream continuum, stream alteration, trophic ecology, warmwater stream

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On a évalué l'impact de l'enlèvement de la végétation riveraine et de la rectification du tracé de chenaux, ainsi que de la variation du régime de débit, sur la structure trophique, le succès de la reproduction et le taux de croissance des poissons dans un cours d'eau d'amont naturel (Jordan Creek; JC) et un cours d'eau d'amont modifié (Big Ditch; BD) du centre-est de l'Illinois. Il y a eu une plus forte augmentation des habitats peu profonds et des substrats organiques dans BD que dans JC pendant les périodes de débit réduit en été. La densité des insectes dans JC était plus élevée à la fin du printemps, pour atteindre de bas niveaux à la fin de l'été. La densité des insectes dans BD était élevée pendant tout l'été. Les poissons dans JC étaient en majeure partie des insectivores benthiques et des insectivores–piscivores; les structures trophiques et d'âge et la biomasse étaient stables d'une année et d'une saison à l'autre; les recrues, principalement des insectivores–piscivores et des insectivores généralisés, constituaient une petite partie stable de la biomasse de la communauté; et les plus jeunes classes d'âge occupaient les habitats peu profonds en eau rapide. Les poissons adultes et les recrues dans BD étaient en majeure partie des insectivores généralisés, des omnivores et des herbivores–détritivores; cex deux derniers types étaient surtout constitués d'espèces vivant au milieu du cours d'eau (*Carpoides cyprinus* et *Dorosoma cepedianum*). Des variations saisonnières annuelles considérables de la structure trophique, de la biomasse totale et de la structure d'âge ont eu lieu dans BD. Celles-ci étaient associées à des variations annuelles du régime de débit, l'abondance des substrats organiques et le succès de reproduction des espèces vivant au milieu du cours d'eau. Les plus jeunes classes d'âge avaient des taux plus élevés de croissance dans BD par rapport à JC. Les variations temporelles de l'environnement physique et l'instabilité de la base d'énergie autotrophique créée dans les cours d'eau d'amont

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modifiés sont probablement les principaux facteurs ayant entraîné les modifications récentes des grandes communautés de poissons et des rivières du Middle West américain, où les espèces insectivores et insectivores–piscivores ont été remplacées par des espèces omnivores et herbivores–détritivores.

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APPROXIMATELY 5.5 to 6.5 million km of streams exist in the United States of which 85% are small headwaters of 1st to 3rd order (Leopold et al. 1964). Of these small streams, ~65 000 km have undergone alteration (A. D. Little, Inc., Council on Environmental Quality, Washington, DC, 1973), usually involving both channel morphology and riparian vegetation. Numerous excellent studies have documented changes in invertebrate and fish communities that result from stream alterations (Schneberger and Funk 1971; Menzel and Fierstine 1976; Griswold et al. 1978). However, no intensive studies have documented the interactions of flow regime, channel morphology, and energy base of the stream ecosystem and their association with fish community structure and function in natural and modified streams. This integrative approach is essential for establishing appropriate management strategies (Karr and Schlosser 1978; Karr and Dudley 1981; Schlosser 1982). In this paper I examine 3 yr of data on the influence of flow regime, habitat structure, and resource dynamics on trophic structure, reproductive success, and growth rate of fishes in a natural and modified headwater stream in east-central Illinois. These results are discussed in light of the stream continuum concept (Cummins 1975; Vannote et al. 1980).

Methods and Materials

STUDY AREAS

Jordan Creek (JC), a second-order stream in Vermilion County, Illinois (Fig. 1), drains a glaciated area of 25–30 km^2. Topography is level in the upper portion of the basin but rolling in the lower regions (Schlosser and Karr 1981a; Schlosser 1982). Dominant land use (80%) is row crop agriculture (Schlosser and Karr 1981a). Sampling for this study was restricted to the lower part of the stream near the Salt Fork River. The natural high gradient channel in this area (4 m/km) has well-developed pools, undercut banks, large rocky riffles, and an average width of 5–6 m. Riparian vegetation (10–400 m wide) consists of maple (*Acer*), oak (*Quercus*), cottonwood (*Populus deltoides*), and sycamore (*Plantanus occidentalis*). Total phosphorus levels during base flow periods are normally 0.03–0.05 mg/L (Schlosser and Karr 1981b). Nitrate levels are variable because of seasonal fluctuations in groundwater flow, but ranged from 3 to 8 mg/L.

Big Ditch (BD) is a channelized, third-order stream in Champaign County, Illinois (Fig. 1) draining a glaciated area of 75–85 km^2 (Schlosser and Karr 1981b). Topography is level in the upper portion of the basin but rolling near the Sangamon River. Municipal wastewater inputs of ~75 million L/d from the city of Rantoul enter the upper portion of the stream. Seasonal and spatial changes in water quality below this input have been previously documented (Schlosser and Karr 1981b). Fish and invertebrate sampling was restricted to the area below the major impact of toxic substances emitted by the wastewater plant. However, phosphorus levels in the study area were high (total P/0.3–0.5 mg/L; Schlosser and Karr 1981b). Nitrate levels were similar to those in JC. The moderate gradient channel in BD (1.5 m/km) has an average width of 5–7 m and consists primarily of shallow raceway habitats with intermediate depth and current velocity (Winn 1958). Channel substrates are sand, gravel, and rock. Riparian vegetation is absent because of cultivation to the stream edge. Land use (90%) is row crop agriculture (Schlosser and Karr 1981b).

HABITAT STRUCTURE

Habitat was measured in three dimensions: depth, current, and substrate (including inorganic and organic materials). Protocol for measuring habitat structure, along with the categories recorded for the three dimensions, followed Schlosser (1982) as adapted from Gorman and Karr (1978).

INVERTEBRATE SAMPLING

Monthly drift samples were taken April–August in both streams in 1979 and 1980. Using the procedure outlined by Schlosser (1982), drift was sampled for 1 h within the first 2 h after dusk (the period of maximum drift in central Illinois streams — Larimore 1974).

Benthic invertebrates were sampled during spring and summer 1980. Two artificial substrates (Hester–Dendy samplers) were placed in a riffle and raceway in each stream. The samplers consisted of nine round ceramic plates spaced 4 mm apart with a total surface area of 0.09 m^2. Substrates were put into the stream on May 15 and replaced on July 7; the latter were removed on August 20.

Invertebrates were subsampled using the procedure described by Waters (1969). Chi-square analyses indicated no difference ($P > 0.05$) in distribution of insect orders between subsamples and total sample. Coefficient of variation for total number of individuals per subsample was ~7%. One-eighth of each sample was sorted to order and counted.

FISH SAMPLING

Fish were sampled twice a year (in May–June and August–September) over a 3-yr period (1978–80). Five reaches, each 100 m in length, were sampled in JC. In 1979 and 1980 each habitat type (i.e. pool, raceway, and riffle) was sampled separately to document habitat use pattern for each size class and species. Six stations, each 100 m in length, were sampled in BD. Habitat specific sampling was not conducted in BD because of the uniform channel.

Fish in JC were sampled with an electric seine 7 m in length powered by a generator with a maximum capacity of 8.7 A of 60-cycle alternating current. The sampling procedure for JC and its efficiency have been previously reported (Larimore

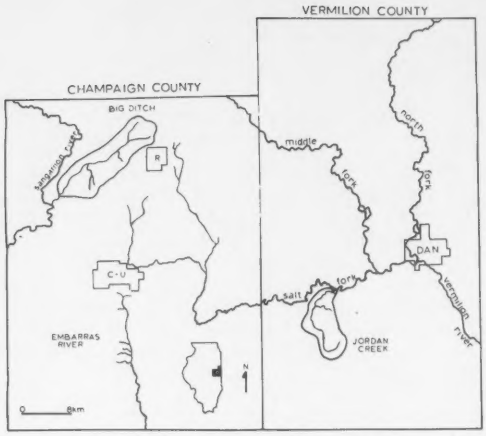


FIG. 1. Location of Jordan Creek and Big Ditch drainage basins (Illinois); C–U = Champaign–Urbana, R = Rantoul, DAN = Danville.

1961; Schlosser 1982). Stations in BD with a uniform bottom were sampled with a minnow seine (1.2 m × 6 m, 4.8-mm mesh). Block seines were placed at upper and lower ends, and stations were divided into smaller sections of 30–50 m. Each section was repetitively seined until capture rates declined to near zero (Schlosser 1982). Sites in BD with poorly developed pools or riffles were sampled with an electric seine according to the procedure outlined for JC.

To ensure that conclusions were not due to differences in sampling methods, two stations with a uniform bottom were electroseined after drag seining. Electroseining increased number of fish caught by <1% and biomass by <5%, indicating that drag seining missed few fish. Neither drag seining nor electroseining were effective at capturing fish below 20 mm in length.

Most fish were measured in the field to the nearest millimetre and released. Weights were estimated using length–weight regressions. Regressions were calculated from lengths and weights of fish collected throughout the year. All regression equations explained more than 97% of variation in weight. Biomass values were based on wet weight.

FISH TROPHIC GROUPS

Fish were classified into one of five trophic groups based on personal and published sources (Carlander 1969, 1977; Pflieger 1975; Karr and Dudley 1978; Smith 1979). Herbi-

TABLE 1. Names and trophic classification of fish species in Jordan Creek and Big Ditch. Trophic groups: herbivore–detritivore (HD), omnivore (OMN), generalized insectivore (GI), surface and water column insectivore (SWI), benthic insectivore (BI), and insectivore–piscivore (IP).

Common name	Scientific name	Trophic classification
Gizzard shad	*Dorosoma cepedianum*	HD
Grass pickerel	*Esox americanus vermiculatus*	IP
Central stoneroller	*Campostoma anomalum*	HD
Common carp	*Cyprinus carpio*	OMN
Hornyhead chub	*Nocomis biguttatus*	GI
Striped shiner	*N. chrysocephalus*	GI
Bigmouth shiner	*N. dorsalis*	OMN
Spotfin shiner	*N. spilopterus*	SWI
Sand shiner	*N. stramineus*	OMN
Redfin shiner	*N. umbratilus*	SWI
Bluntnose minnow	*Pimephales notatus*	OMN
Fathead minnow	*P. promelas*	OMN
Creek chub	*Semotilus atromaculatus*	GI
Quillback	*Carpiodes cyprinus*	OMN
White sucker	*Catostomus commersoni*	BI
Creek chubsucker	*Erimyzon oblongus*	BI
Northern hog sucker	*Hypentelium nigricans*	BI
Golden redhorse	*Moxostoma erythrurum*	BI
Yellow bullhead	*Ictalurus natalis*	BI
Stonecat	*Noturus flavus*	BI
Backstripe topminnow	*Fundulus notatus*	SWI
Rock bass	*Ambloplites rupestris*	IP
Green sunfish	*Lepomis cyanellus*	IP
Bluegill	*L. macrochirus*	IP
Longear sunfish	*L. megalotis*	IP
Smallmouth bass	*Micropterus dolomieui*	IP
Greenside darter	*Etheostoma blennioides*	BI
Rainbow darter	*E. caeruleum*	BI
Fantail darter	*E. flabellare*	BI
Johnny darter	*E. nigrum*	BI
Orangethroat darter	*E. spectabile*	BI

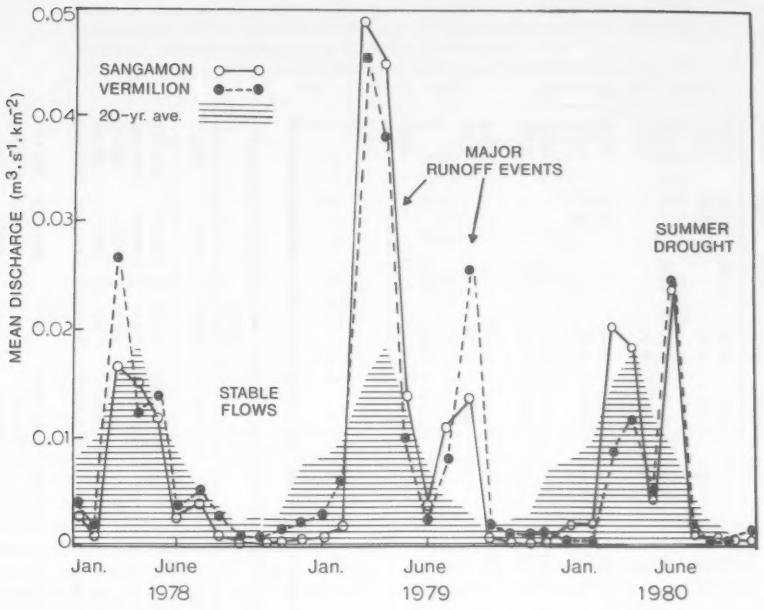


FIG. 2. Temporal variation in mean discharge ($m^3 \cdot s^{-1} \cdot km^{-2}$) during the 3-yr sample period at the USGS gauging station nearest Big Ditch (Sangamon River) and Jordan Creek (Vermilion River). The 20-yr average (1961–80) was nearly identical for the two stations and was plotted for the Vermilion River.

vore–detritivores (HD) fed almost entirely on diatoms or detritus. Omnivores (OMN) consumed both plant and animal material; subjectively, >25% of the diet was plant material. Generalized insectivores (GI) ingested a range of animal and plant material, including terrestrial and aquatic insects, attached algae, and small fishes by larger individuals; subjectively, <25% of their diet was composed of plant material or detritus. Surface and water column insectivores (SWI) fed on drift in the water column or terrestrial insects at the water surface. Benthic insectivores (BI) ingested predominantly immature benthic insects. Insectivore–piscivores (IP) fed on a variety of aquatic invertebrates and small fish. Piscivory varied from almost complete piscivory (*Esox americanus*) to large amounts of invertebrates (*Lepomis* spp.). Species captured in JC and BD are listed in Table 1.

GROWTH RATES

Absolute growth rates (g/d) for age-group 0 and I were calculated from length–frequency distributions. Sample sizes ranged from 50 to several hundred individuals. Overlap between age-groups existed but young age-groups were sufficiently distinct that overlap was minimal. Absolute growth rates for age 0 individuals were based on size at capture and spawning dates estimated to the nearest 2 wk. Spawning dates were based on personal observation and the literature (Pflieger 1975; Smith 1979).

Results

FLOW REGIME

Temporal variation in discharge was similar in both streams (Fig. 2) during the 3-yr sample period. Near normal flow conditions persisted throughout 1978 with decreasing flows during summer months. Spring discharges were above normal in 1979 because of heavy winter snowfall and near-record rainfall in April. Three periods of elevated discharge occurred in July–August 1979. Near-normal flow conditions persisted in 1980 until high flows occurred in June. A drought resulted in low flows in summer 1980.

HABITAT STRUCTURE

Habitat structure and the abundance of organic matter during summer periods fluctuated between years because of variable flow conditions.

Depth was more variable temporally in BD than JC (Table 2). Deep habitats (>50 cm) were more common in JC than BD on all sample dates (Table 2). Shallow (5–20 cm) and moderate (20–50 cm) depths were found in similar proportions in JC and small shifts from moderate to shallow depths occurred during low flow years (1978, 1980). Large fluctuations in depth occurred in BD because of the uniform channel (Table 2). Deepwater habitats (>50 cm) were

TABLE 2. Proportion of habitat in each depth, current, and substrate category in Big Ditch and Jordan Creek.

		Depth (cm)				Current m(s)			Substrate					
Stream	Date	0–5	5–20	20–50	>50	≤0.3	0.3–1.5	>1.5	Silt	Sand/ gravel	Pebble/ rock	Algae	Litter	Other
Jordan	June 1978	0.01	0.40	0.51	0.08	0.53	0.40	0.07	0.07	0.33	0.33	0.20	0.02	0.05
	Aug. 1978	0.06	0.44	0.44	0.06	0.87	0.10	0.03	0.10	0.37	0.39	—	0.08	0.06
Big Ditch	June 1978	—	0.23	0.75	0.02	0.39	0.47	0.14	0.23	0.43	0.22	0.08	—	0.04
	Aug. 1978	0.08	0.74	0.18	—	0.94	0.06	—	0.60	0.25	0.12	—	—	0.03
Jordan	June 1979	0.02	0.39	0.51	0.08	0.65	0.27	0.08	0.07	0.39	0.40	—	0.01	0.13
	Aug. 1979	0.01	0.34	0.55	0.10	0.63	0.27	0.10	0.03	0.40	0.43	—	0.01	0.13
Big Ditch	June 1979	—	0.20	0.76	0.04	0.40	0.45	0.15	0.18	0.54	0.17	0.02	—	0.09
	Aug. 1979	—	0.43	0.53	0.04	0.50	0.38	0.12	0.09	0.64	0.18	0.01	—	0.08
Jordan	June 1980	0.02	0.41	0.48	0.09	0.69	0.26	0.05	0.03	0.46	0.37	—	—	0.14
	Aug. 1980	0.04	0.49	0.39	0.08	0.95	0.05	—	0.04	0.45	0.36	—	—	0.15
Big Ditch	June 1980	0.01	0.40	0.57	0.02	0.41	0.52	0.07	0.19	0.53	0.06	0.22	—	—
	Aug. 1980	0.05	0.66	0.29	—	0.89	0.11	—	0.14	0.41	0.15	0.24	—	0.06

TABLE 3. Numbers of nymphs (pupae plus adults in parentheses) per 100 m^3 in drift of Jordan Creek and Big Ditch. Other insect orders combined comprised much less than 1% of total numbers. nd = No data.

		1979					1980				
Stream	Taxa	April	May	June	July	Aug.	April	May	June	July	Aug.
Jordan Creek	Diptera	68(150)	98(370)	111(902)	15(111)	18(107)	152(933)	1103(5060)	131(69)	104(45)	105(131)
	Ephemeroptera	15(0)	42(0)	50(195)	65(5)	168(19)	2(0)	1735(0)	81(6)	446(45)	145(144)
	Trichoptera	6(0)	8(0)	72(31)	10(5)	18(0)	7(0)	0(39)	45(9)	30(0)	26(0)
	Coleoptera	11(7)	0(16)	15(15)	0(36)	0(0)	2(0)	0(0)	0(9)	30(89)	26(13)
	Total	100(157)	148(386)	248(1143)	90(157)	204(126)	163(933)	2838(5099)	257(93)	610(179)	302(288)
Big Ditch	Diptera	88(41)	25(90)	123(1034)	nd	153(45)	134(290)	866(3068)	nd	288(446)	205(137)
	Ephemeroptera	14(0)	0(0)	66(113)	nd	275(9)	12(0)	140(0)	nd	5472(173)	634(0)
	Trichoptera	0(0)	0(0)	0(0)	nd	18(0)	4(0)	58(0)	nd	14(0)	62(0)
	Coleoptera	0(0)	0(4)	0(10)	nd	0(18)	0(0)	5(19)	nd	0(0)	62(51)
	Total	102(41)	25(94)	189(1157)	nd	446(72)	150(290)	1069(3087)	nd	5774(619)	963(188)

TABLE 4. Seasonal and spatial variation in the abundance (no./m^2) of Diptera (DPT), Ephemeroptera (EPH), Trichoptera (TRI), and Coleoptera (COL) on artificial substrates in raceway and riffle habitats in Big Ditch and Jordan Creek.

		May 15–July 8, 1980		July 9–Aug. 20, 1980	
Stream	Taxa	Raceway	Riffle	Raceway	Riffle
Big Ditch	DPT	1333	2555	777	1505
	EPH	4711	3577	5677	2950
	TRI	1444	6866	911	2783
	COL	22	67	78	—
	Total	7510	13065	7443	7238
Jordan Creek	DPT	289	1244	467	778
	EPH	1022	600	239	78
	TRI	778	1711	50	206
	COL	—	44	6	6
	Total	2089	3599	762	1068

uncommon and present only during high flow conditions in 1979. Large shifts from intermediate (20–50 cm) to shallow (5–20 cm) depths occurred during low flow conditions (1978, 1980).

Very fast currents (>1.5 m/s) were more common in BD than JC under stable or high flow conditions because of unimpeded flow through the straight channel (Table 2). Shifts toward very slow currents (<0.3 m/s) occurred in both streams during low flow conditions.

Seasonal and annual shifts in substrate in the streams reflected differences in primary production during summer and annual variation in flow regime. Substrates in JC were constant between both seasons and years (Table 2). Algae abundance was high in JC in spring 1978 but was absent by August because of shading by riparian vegetation. Little organic buildup occurred in JC during summer periods. Seasonal and annual shifts in substrates occurred in BD. Substrates shifted from sand and gravel to "silt" during the low flows of 1978. The silty material was a thick mat of inorganic and organic ooze along with diatoms (primarily *Navicula* and *Nitzschia*). Fine inorganic and organic particles were apparently filtered from the water column by the developing periphyton. Substrates did not shift in 1979 (Table 2) because elevated flows prevented an organic buildup. Low flows persisted throughout the summer of 1980 and a large standing crop of filamentous algae (*Cladophora*) was present. The cause of the shift from diatomaceous primary production in 1978 to filamentous production in 1980 was probably a change in water chemistry or temperature (Patrick et al. 1969). Nutrient levels did not appear to differ between 1978 and 1980 (Schlosser and Karr 1981b; Schlosser unpublished data) although water temperature was substantially higher in 1980 (frequently >30°C), suggesting that a between-year difference in temperature regime was probably responsible for the shift in nature of organic production (Patrick et al. 1969).

INSECT ABUNDANCE

The most appropriate indicator of insects available to the fish community will vary depending on the trophic group. For surface and water column insectivores drift rate is probably most appropriate, while for benthic insectivores the rate of benthic production would be most suitable. The time required to measure benthic insect production would have been prohibitive. Rather, presence of immature and mature insects in the drift and density of immature forms on artificial substrates were used as indicators of insects available to the fish community.

Insect abundances in the drift reflected spring emergence, differences in seasonal dynamics of the organic energy base, and annual variation in flow regime (Table 3). Both streams had peak numbers of mature forms (pupae plus adults) drifting in late spring or early summer (May–June). Spring emergence was lower in BD than JC in both years. Abundance of immature and mature forms was lower in spring 1979 than 1980 and was associated with large runoff events in March–April 1979. Spring drift was predominantly Diptera in both streams. Ephemeroptera and Trichoptera were more abundant in JC than BD in spring (Table 3).

Drift declined in summer (July–August) relative to spring in both streams in 1979 (Table 3). Summer drift rates in 1979 were similar in the two streams. Low flows persisted in 1980 and a substantial buildup of organic substrates occurred in BD. Drift of immature forms decreased in JC from spring to summer 1980 because of decreased drift of Diptera and Ephemeroptera. Drift of immature forms in BD did not decrease during summer months because of increased abundances of Ephemeroptera. Drift was higher in BD than JC for all insect orders during August 1980 (Table 3).

Benthic insect densities were higher in BD than JC across all insect orders, habitats, and sampling dates (Table 4). Insect densities declined in raceway and riffle habitats from early summer to late summer. Large decreases in Trichoptera occurred in riffle habitats (Table 4). Most Trichoptera were net-spinning collector–filterers of suspended organic matter (Hydropsychidae; Merritt and Cummins 1978). Low flows in late summer 1980 were probably responsible for the decrease in this trophic group. Ephemeroptera, especially Caenidae and Baetidae, dominated the insect fauna in BD raceways (Table 4). These taxa are collector–gatherers of organic matter or scrapers of primary production (Merritt and Cummins 1978). High insect densitites on artificial substrates in BD were not due to a lack of other habitat suitable for colonization. Habitats in BD and JC raceways had similar

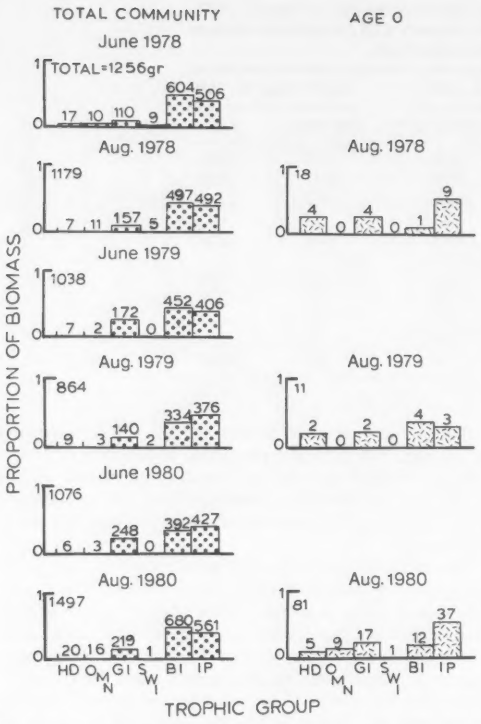


FIG. 3. Seasonal and annual variation in trophic structure for the total community and age group 0 in Jordan Creek. Numbers represent biomass (g/100 m^2). Trophic groups: herbivore–detritivore (HD), omnivore (OMN), generalized insectivore (GI), surface and water column insectivore (SWI), benthic insectivore (BI), and insectivore–piscivore (IP).

depths, substrates, and current velocities. Surber samples taken in the two streams also indicated large differences in insect densitites (Schlosser unpublished data).

FISH TROPHIC STRUCTURE — JORDAN CREEK (JC)

Fish in JC were predominantly benthic insectivores and insectivore–piscivores (Fig. 3). Generalized insectivores made up a small proportion of the fauna. Surface and water column insectivores, omnivores, and herbivore–detritivores were minor components of the community. Recruits (age 0) were primarily insectivore–piscivores, generalized insectivores, and benthic insectivores in 1978 and 1980 (Fig. 3). Trophic structure shifted towards benthic insectivores in 1979 because of adverse impacts of high flow regimes on reproduction in insectivore–piscivores. Recruit biomass contributed little to total community biomass.

Community trophic structure was stable across both seasons and years (Fig. 3). Total biomass decreased during summer months in 1978 and 1979 in association with decreased invertebrate abundance in summer. Biomass increased from June through August during drought conditions in 1980. Upper JC had very low flows in 1980 and large fish in these areas were probably forced into downstream areas with larger pool habitats.

Recruitment (age 0) varied in association with flow regime (Fig. 3). Recruitment was lowest during high flow regimes of 1979 and highest during low flow conditions of 1980, with intermediate levels in 1978. Relatively stable or low flows in 1978 and 1980 favored reproduction especially in insectivore–piscivores and generalized insectivores.

Recruits (age 0) of insectivore–piscivores were most abundant in shallow riffles (Fig. 4) while older age-groups (I–III+) occurred predominantly in pool habitats. Age-groups 0–II of generalized insectivores were primarily in shallow riffles. Only older age-groups of generalized insectivores (III+) were found in deeper pool habitats with large insectivore–piscivores. Spatial distributions were similar in 1980 for age-groups 0 and I in both trophic groups. A greater proportion of older individuals (II and III+) was restricted to deeper habitats (Fig. 4) during low flow conditions in 1980.

FISH TROPHIC STRUCTURE — BIG DITCH (BD)

Seasonal and annual variation in biomass and trophic structure occurred in BD because of shifts in both amount and type of instream organic production. Three periods of intense primary production appeared to occur based on abundance of organic substrates; high diatom production in summer 1978 and high filamentous algae production in late spring and summer 1980 (Table 2).

Total biomass and trophic structure reflected these seasonal and annual shifts in abundance of organic matter (Fig. 5). Total biomass was highest in August 1978 and June and August 1980. Fish biomass increased threefold from June to August 1978 with increases in all trophic groups. Trophic structure shifted towards species strictly using primary production as an energy base, especially age 0 gizzard shad (*Dorosoma cepedianum*). Omnivores were primarily age 0 quillbacks (*Carpoides cyprinus*).

High flows persisted throughout summer 1979 and total biomass decreased (Fig. 5). Fish were predominantly generalized insectivores and no shift in trophic structure to herbivore–detritivores occurred.

High production of filamentous algae in spring and summer 1980 resulted in high and fairly constant fish biomass throughout the summer (Fig. 5). Biomass was higher in all trophic groups in 1980 than 1979. No shift in trophic structure towards herbivore–detritivores occurred. Filamentous algae were unsuitable for direct consumption by herbivore–detritivores which prefer to ingest organic ooze or diatomaceous material (Carlander 1969). Instead, intense algae production supported high invertebrate abundances (Table 4), and generalized insectivores and benthic insectivores were most abundant (Fig. 5).

Age 0 standing crop in BD was highest during stable flow conditions in 1978 and 1980 (Fig. 5) and comprised a large proportion (20–50%) of total community biomass during low flow conditions. Recruits were more abundant in all trophic groups in BD than JC. Total biomass of recruits in BD was 5–50 times greater than JC.

Trophic composition of recruits in BD (generalized insectivores, omnivores, and herbivore–detritivores) differed from

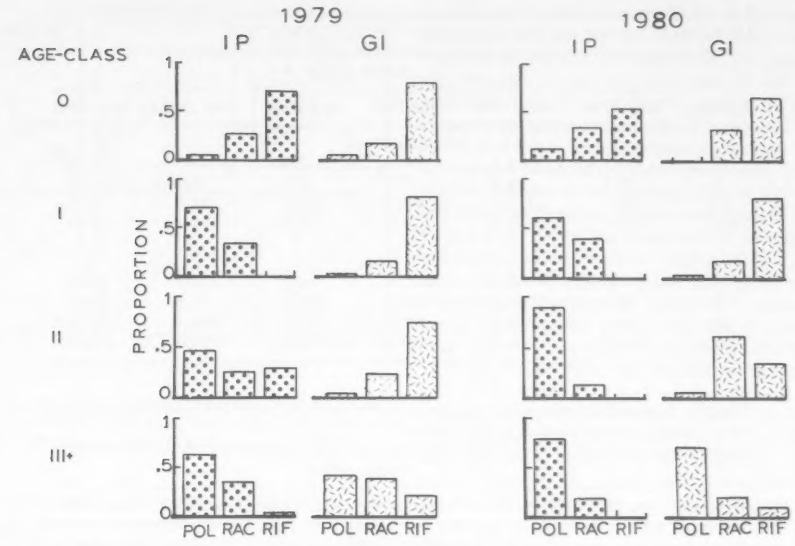
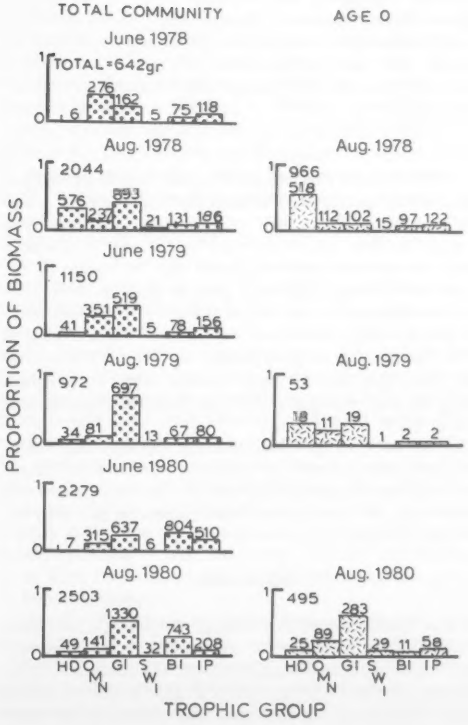


FIG. 4. Spatial distribution in pool, raceway, and riffle habitats of insectivore–piscivore (IP) and generalized insectivore (GI) age groups in Jordan Creek in 1979 and 1980.



that in JC. Insectivores and insectivore–piscivores were smaller components of recruit production than other trophic groups. Recruits were predominantly herbivore–detritivores in 1978 (Fig. 5) because of a summer influx of age 0 gizzard shad to exploit diatom production. Omnivore recruits were primarily quillbacks. Total recruit production in 1980 was lower than 1978 because of the absence of gizzard shad. Recruits were primarily generalized insectivores and omnivores in 1980.

AGE STRUCTURE

Changes in recruitment dynamics and depth had major effects on the dynamics of age structure in the two streams. Age structure for both generalized insectivores (Table 5) and insectivore–piscivores (Table 6) was relatively stable in JC. Abundance of younger age-groups varied between years because of the impact of runoff events on reproductive success. However, the proportion of biomass in each age-group was relatively constant with most of the biomass in older age-groups.

Age structure fluctuated more in BD than JC (Tables 5 and 6). Age 0 generalized insectivores varied temporally in conjunction with stable flows and high reproductive success in 1978 and 1980 (Table 5). Older age-groups (I and II+) fluctuated erratically, reflecting increased emigration and/or mor-

FIG. 5. Seasonal and annual variation in trophic structure for the total community and age group 0 in Big Ditch. Numbers represent biomass (g/100 m^2). Trophic groups: herbivore–detritivore (HD), omnivore (OMN), generalized insectivore (GI), surface and water column insectivore (SWI), benthic insectivore (BI), and insectivore–piscivore (IP).

TABLE 5. Temporal variation in age structure of generalized insectivores in Jordan Creek and Big Ditch. Values represent standing crop (g/100 m^2).

	Sample period					
Age-class	June 1978	Aug. 1978	June 1979	Aug. 1979	June 1980	Aug. 1980
			Jordan Creek			
0	—	4.4	—	2.0	—	17.0
I	27.3	34.9	7.3	9.4	4.9	10.6
II+	82.7	117.7	164.7	128.6	243.1	191.4
Total	110.0	157.0	172.0	140.0	248.0	219.0
			Big Ditch			
0	—	97.1	—	19.2	—	287.5
I	80.9	288.8	82.0	504.5	27.5	205.5
II+	81.1	507.1	437.0	192.5	609.5	837.0
Total	162.0	893.0	519.0	716.2	637.0	1330.0

TABLE 6. Temporal variation in age structure of insectivore–piscivores in Jordan Creek and Big Ditch. Values represent standing crop (g/100 m^2).

	Sample period					
Age-class	June 1978	Aug. 1978	June 1979	Aug. 1979	June 1980	Aug. 1980
			Jordan Creek			
0	—	9.0	—	3.0	—	37.0
I	31.6	22.8	8.2	20.5	4.8	4.6
II+	445.4	400.5	356.4	314.3	373.4	379.2
Total	477.0	432.3	364.6	337.8	378.2	420.8
			Big Ditch			
0	—	122.0	—	2.0	—	58.0
I	2.8	18.9	3.0	0.3	4.6	8.0
II+	114.8	45.1	153.0	77.7	505.4	144.0
Total	117.6	186.0	156.0	82.7	510.0	210.0

tality during winter months and immigration during summer periods of high resource availability. Abundance of older age-groups (II+) was not reduced by shallow depths in late summer (Table 5).

Age structure of insectivore–piscivores in BD varied considerably. Age 0 individuals were abundant during relatively stable flow periods in 1978 and 1980. Age 0 individuals were more abundant in BD than JC, reflecting the predominance of shallow water areas and increased resource availability in BD. However, few recruits survived the winter to age I (Table 6). Age I insectivore–piscivores were more abundant in JC than BD (Table 6) on all sample dates except 8/80. Older age-groups of insectivore–piscivores (II+) in BD were especially susceptible to seasonal changes in flow regimes because of the absence of temporally stable pool habitats. Large individuals entered the stream in spring to spawn, but decreased in abundance during low flow regimes in summer. Similar reductions in abundance of older age-classes in late summer were observed in other pool species (e.g. Catastomidae).

GROWTH RATES

Growth rates of age 0 individuals were greater ($P < 0.01$; Wilcoxon paired sample test) in BD than JC in 1978 and 1980 (Fig. 6). Growth rates in 1979 were marginally different ($P = 0.055$) in the two streams. Growth rates in BD did not appear to be accentuated in any particular trophic group (Fig. 6). However, over the 3 yr of sampling, growth rates in a large benthic omnivore (quillback) and herbivore–detritivore (gizzard shad) suggested that the nature of the organic production influenced growth rates in these species. Growth rates for age 0 quillback in 1978 and 1980 were 159 and 119 mg/d. Successful reproduction did not occur in 1979. Growth rates in age 0 gizzard shad from 1978 to 1980 were 364, 169, and 77 mg/d. Growth rates were highest during the shift in organic substrates towards diatomaceous ooze in 1978.

Growth rates for age I individuals in BD were only calculated for a limited number of species (5–6) because of insufficient number of individuals captured. The basic pattern was similar (Fig. 6); growth rates were greater in BD than JC, with the difference in growth rates being the least in 1979.

Discussion

These results indicate that channel morphology, the nature and seasonal dynamics of the organic energy base, and seasonal fluctuations in discharge interact to determine trophic structure, reproductive success, and growth rate of stream fishes. Segregating the individual and interactive role these

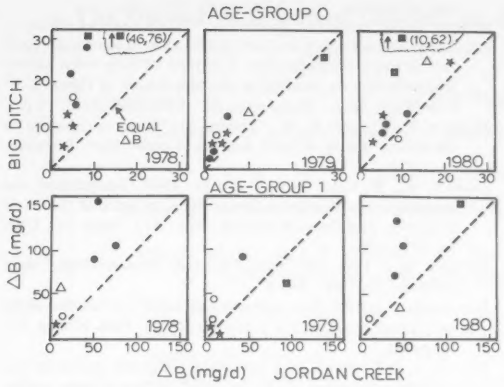


FIG. 6. Absolute growth rates (mg/d) in Jordan Creek versus Big Ditch for age 0 and I individuals during the summer period over the 3 yr of sampling; ● (GI), ○ (OMN), ★ (BI), ▲ (HD), ■ (IP).

factors play in shaping fish communities is essential for establishing ecologically sound management strategies (Karr and Schlosser 1978; Karr and Dudley 1981; C. P. Hawkins et al. unpublished data).

Channel morphology, in conjunction with flow regime, appears to be especially important in determining habitat stability and a broad range of fish community attributes (Schlosser 1982). Large pools in JC increase habitat volume and stability relative to BD, resulting in a trophic structure of predominantly large insectivore–piscivores and benthic insectivores. Small fish and younger age-classes are not abundant and are restricted to shallow riffle and raceway habitats. Trophic structure, age structure, and production of recruits are stable in JC. This contrasts with BD which has large expanses of shallow habitats that exhibit substantial fluctuations in depth. Large pool-dwelling species are less abundant and enter the stream only in spring to spawn during periods of high discharge. Small fish species (generalized insectivores) and younger age-classes are the predominant component of the community. The abundance of small fish undergoes large annual fluctuations because of the effect of variation in discharge on reproductive success (Starrett 1951; Schlosser 1982). Trophic structure, age structure, and production of recruits are temporally variable, associated with habitat instability and fluctuations in reproductive success. These differences in fish community dynamics in natural and modified headwater streams are consistent with differences along physical gradients from temporally variable upstream and riffle habitats to temporally stable downstream and pool habitats (Schlosser 1982). This suggests that for small warmwater streams in the midwestern United States, qualitatively predictable patterns of fish community structure and function occur along both natural physical gradients and those created by human disturbance.

Alteration of riparian vegetation increases instability in the fish community by shifting the nature and seasonal dynamics of the organic energy base. Organic inputs from riparian vegetation are relatively predictable in natural headwater streams in the eastern United States (Bell et al. 1978). Autochthonous production is a minor component of the organic energy base, especially in summer when extensive shading occurs. Removal of riparian vegetation shifts the energy base from allochthonous to autochthonous material and the period of maximum abundance of organic matter from autumn and winter to late spring and summer. The elevated nutrient levels in BD accentuate the autotrophic production. However, the amount and nature of the autotrophic energy base are highly variable because of the scouring effect of high flow regimes and annual shifts in the physical environment (Whitton 1975; Partick et al. 1969). The importance of this summer pulse of primary production to higher trophic levels is accentuated in these streams as it occurs when the organic energy base is normally low (McIntire and Colby 1978), spawning activities have been completed, and growth rates of young fish appear to be limited by low resource availability (McIntire and Colby 1978; Schlosser 1982). The elevated production at lower trophic levels results in higher invertebrate and recruit abundances and greater growth rates of fishes. Yearly variation in both amount and trophic composition of recruits is substantial, apparently because of the synergistic effect of flow regime on both the organic energy base and reproductive success. Thus, alterations in riparian vegetation accentuate instability of the fish community by creating a large but unstable pulse of resources during the critical summer period.

The effects of these alterations of headwater streams on downstream fisheries are evident when they are placed in the perspective of the stream continuum concept (Cummins 1975; Vannote et al. 1980). This concept hypothesizes that interactions between the physical environment and the organic energy base result in a relatively predictable pattern of lotic community structure and function from headwaters to downstream areas. The critical effect of stream alterations in the context of this concept is that alterations create a shallow, temporally variable physical environment typical of headwater areas where most recruitment occurs (Schlosser 1982). Yet, at the same time, the alterations shift the energy base towards autotrophic processes which are more typical of mid-river habitats (Cummins 1975; Vannote et al. 1980). The result is that large pulses of recruits frequently are predominantly mid-river omnivores and herbivore–detritivores. Land use in headwaters of large river systems, therefore, will have potentially major impacts on trophic structure and stability of fish communities throughout the river system. Stream alterations in headwater areas are probably major factors responsible for the shift in recent decades of many large river communities in the midwestern United States from insectivore and insectivore–piscivore fishes to omnivores and herbivore–detritivores.

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The Impact of Copepod Grazing on the Phytoplankton of Georges Bank and the New York Bight

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DAGG, M. J., AND J. T. TURNER. 1982. The impact of copepod grazing on the phytoplankton of Georges Bank and the New York Bight. Can. J. Fish. Aquat. Sci. 39: 979–990.

The grazing rate of the copepod community was calculated at 10-km intervals on transects of the continental shelf south of Long Island, New York, and across Georges Bank during April, July, and October 1978. During the spring when *Calanus* and *Pseudocalanus* dominated, grazing tended to be greatest on the outer shelf and slope regions, and community ingestion rates never exceeded primary production rates; much of the spring bloom was not grazed. During the fall when *Centropages* and *Oithona* dominated, grazing was greatest in the shallower regions, and community ingestion rates were often equivalent to or slightly greater than primary production rates. About 50% of the annual primary production was grazed by the copepod community in both regions.

Key words: community grazing, Georges Bank, New York Bight, phytoplankton

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Nous avons calculé le taux de broutage de la communauté de copépodes à intervalles de 10 km le long de lignes traversant le plateau continental au sud de Long Island (New York) et le banc Georges en avril, juillet et octobre 1978. Au printemps, alors que *Calanus* et *Pseudocalanus* prédominent, le broutage tend à être maximal dans les régions du large du plateau et des pentes, et les taux de consommation de la communauté ne dépassent jamais les taux de production primaire; une bonne partie de la floraison printannière n'est pas broutée. À l'automne, alors que *Centropages* et *Oithona* prédominent, le broutage est à son maximum dans les régions peu profondes et, souvent, les taux de consommation de la communauté sont égaux ou légèrement supérieurs aux taux de production primaire. Dans les deux régions, environ 50% de la production primaire annuelle est brouté par la communauté de copépodes.

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PRIMARY producers in the pelagic marine realm are either grazed, remineralized, or deposited on the bottom through sinking (e.g. Lorenzen 1976; Harrison 1978), and knowledge of the relative importance of these processes is necessary for understanding food web dynamics (e.g. Steele 1974; Walsh 1981). The grazing link is especially important in understanding the yield of pelagic fish, and yet this link is not well quantified. Partly this is because grazer behavior is complex. For example, food concentration, food quality, temperature, spatial and temporal relationships between food and feeders, and the species and size of grazer are among the many factors which affect feeding rates of individual copepods. Nevertheless it is clear that grazers play a strong role in modifying or controlling phytoplankton populations in the ocean (e.g. Riley and Bumpus 1946; Cushing 1968; Taguchi and Fukuchi 1975; Steele and Frost 1977; Jamart et al. 1979; Sonntag and Parsons 1979; Dagg et al. 1982).

In this paper we calculate, for three seasons, the impact of grazing by the net-caught copepod community on the phytoplankton production in two coastal regions of eastern North America.

Methods

Two regions were studied: a cross-shelf transect south of Long Island, New York, and a transect across Georges Bank. Both transects were occupied three times during 1978, the Long Island transect on April 4–6, June 30–July 1, and October 12–13, and the Georges Bank transect on April 9–11, July 2–3, and October 21–23 (Fig. 1). Each transect

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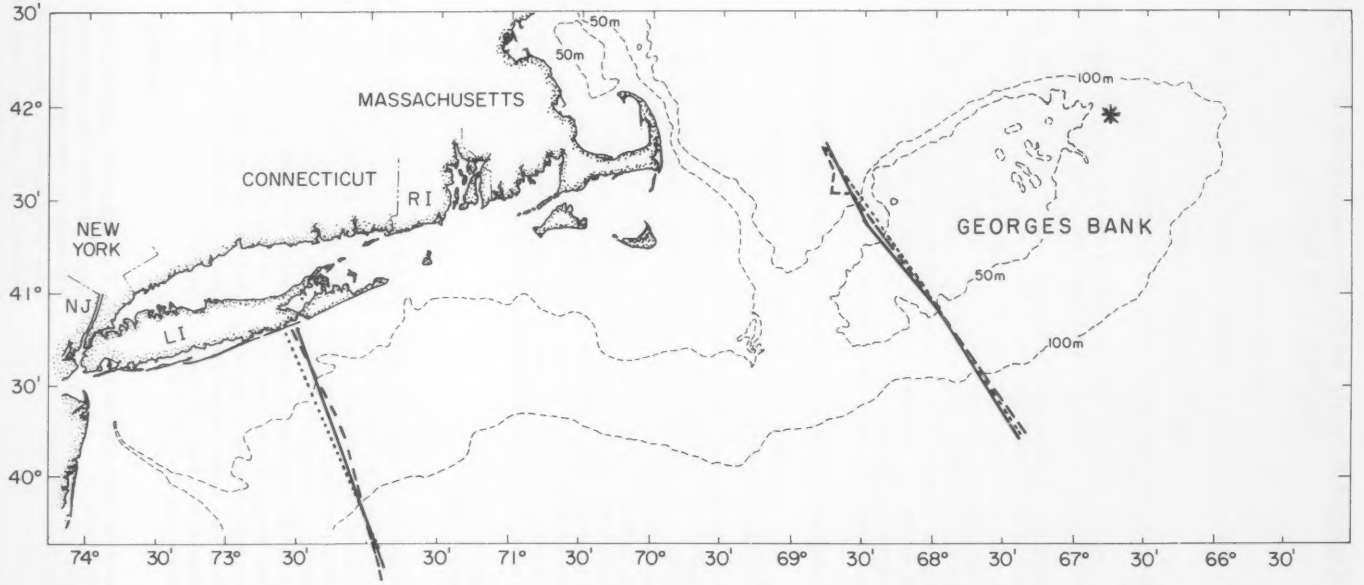

FIG. 1. Locations of transects across the Long Island shelf and Georges Bank during April (solid line), July (broken line), and October (dotted line), 1978. The time–series station on Georges Bank is noted with an asterisk.

TABLE 1. The body weights of copepods considered as grazers in this study.

Species	Stage	Body wt (μg C)
Calanus finmarchicus	Female	116.6
	CV	59.4
Pseudocalanus sp.	Female	11.0
	CV	5.6
Paracalanus parvus	Female	3.0[a]
	CV	1.0[b]
Centropages typicus	Adult	13.1
	CV	6.7
Temora longicornis	Adult	9.8
	CV	5.0[b]
Acartia spp.	Adult	2.5
	CV	1.3[c]
Oithona similis	Adult	2.0

[a]Checkley 1980.
[b]Estimated.
[c]Landry 1978.

included from 13 to 15 stations. During the October cruise two time–series stations were occupied, a 36-h station at about the 60-m isobath on the Long Island transect and a 28-h station at about the 60-m isobath on the northeast corner of Georges Bank.

Zooplankton were sampled in two ways. At each station on the April and July cruises and at most stations on the October cruise, vertical hauls from either a few metres off the bottom or 100 m were made with 102-μm-mesh nets attached to a 60-cm-diameter BONGO net-frame. The amount of water filtered was measured with a General Oceanics flowmeter fitted into the mouth of one of the nets. The contents of one cod-end were preserved in 15% formalin for later quantification. At the two time–series stations and at alternate stations on the Long Island transect during October, zooplankton were sampled every 4 h from discrete depths (0, 5, 10, 15, 20, 25, 35, 45, and 55 m) using a pumping system with a 10-cm-internal-diameter hose, which sampled ~750 L min^{-1}. At each depth the system was flushed and then 3785 L (1000 gallons) of seawater were pumped through a flowmeter and into a 0.5-m-plankton net (102-μm mesh) supported in a large drum on deck. A TSK time–depth recorder was attached to the hose intake for verification of sampling depths. For a more complete description of this pumping system see Miller and Judkins (1981).

In the laboratory, five aliquots were removed from each sample with a piston pipette. Pipette volume was selected so that each aliquot contained ~300 animals.

Because there is no single piece of gear that will properly sample all sizes and types of zooplankton, some planktonic organisms (e.g. microzooplankton and soft-bodied grazers) that might feed on particles were not considered in this study. Furthermore, of the organisms caught in our nets only the abundant copepods were considered as grazers. This does not cause a major underestimation of the total copepod abundance because the net-caught zooplankton in these regions consist mainly of a few species (Judkins et al. 1979; Grice and Hart 1962). Furthermore, many of the ignored zooplankters are very small; the copepod biomass is almost fully represented

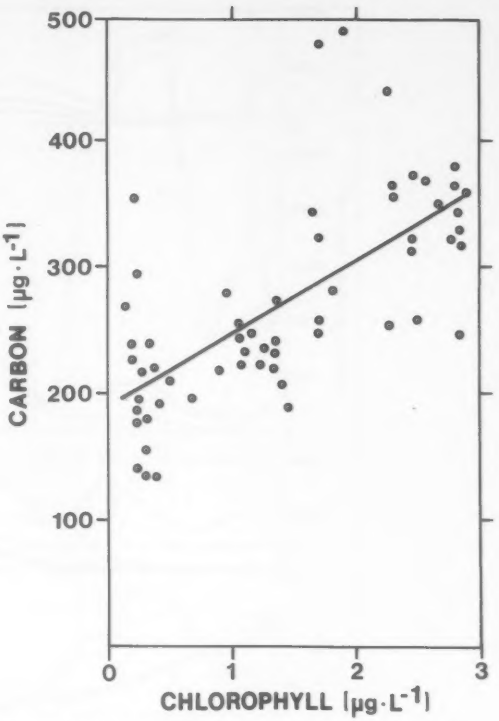

FIG. 2. Relationship between particulate carbon (PC) and chlorophyll determined during October 1978. PC = 191.7 + 57.8 (chl), $n = 60$, $r^2 = 0.46$.

by the few species listed in Table 1. Males of *Calanus finmarchicus*, *Pseudocalanus* sp., and *Paracalanus parvus* are excluded because they are short-lived and considered to be weak feeders (Marshall and Orr 1955; D. Checkley, Univ. Texas Marine Lab, Port Aransas,TX 78373, personal communication; G. Paffenhöfer Skidaway Institute, Savannah, GA 31406, personal communication). Late copepodid stages of each species were not separately counted and are assumed to be stage V.

The body size of most of the copepod grazers (Table 1) was determined by sorting, drying in an oven at 50–60°C, and later weighing representative specimens on a Cahn electrobalance (model G-2). The carbon content of each sample was measured with a Carlo-Erba CHN analyzer (model 1104).

The incorporation of all the factors which affect the grazing rate of an individual into a field calculation is impractical. Conversely it is an oversimplification to treat the grazing behavior of all individuals as identical (Frost 1980; Mullin and Brooks 1976). As a compromise, feeding rates of individual copepods were calculated using equations which relate the ingestion of *Calanus pacificus* to body size and food concentration:

$$I = (7.3 \times 10^{-4})\, pW^{0.35} \text{ for } p \leq 57W^{0.35}$$

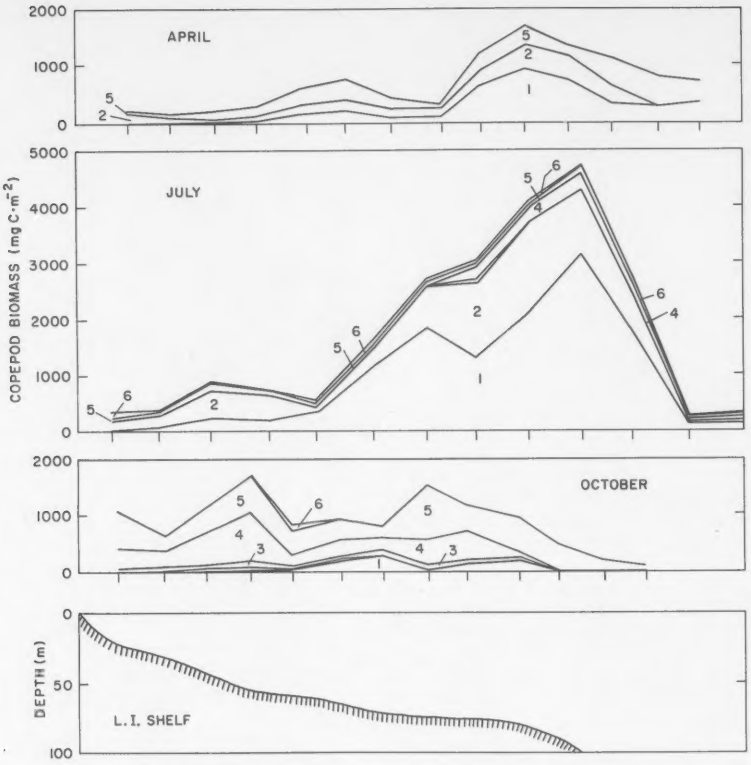

FIG. 3. Biomass of grazing copepods on the Long Island transect. 1, *Calanus finmarchicus*; 2, *Pseudocalanus* sp.; 3, *Paracalanus parvus*; 4, *Centropages typicus*; 5, *Oithona similis*; and 6, others (*Temora longicornis* and *Acartia* spp.).

and

$$I = (41.6 \times 10^{-3})\, W^{0.7} \text{ for } p > 57W^{0.35}$$

where I is ingestion as μg C·h^{-1}, p is food concentration as μg C·L^{-1}, and W is copepod weight as μg C (Mullin and Brooks 1976). Feeding experiments in natural seawater have shown that these equations reasonably describe the feeding behavior of at least some other copepods besides *C. pacificus* (Dagg and Grill 1980; Dagg et al. 1982), although it is unlikely they will be applicable to all (Frost 1980).

To determine food concentration, seawater collected with Niskin bottles from various depths was analyzed with a Coulter counter, model TA II, fitted with a 280-μm-aperture tube. Each analysis yielded information on the abundance and size frequency distribution of particulate material between 5 and 128 μm equivalent spherical diameter (ESD). This technique divided particulate material into 15 size categories. The organic carbon content of a particle in each size category was calculated using the geometric mean volume of the particle and the equation of Mullin et al. (1966). The food concentration was obtained by summing the carbon contents of all categories.

Chlorophyll was used to determine food concentrations at the two time–series stations. Analyses followed the methodology for extracted in vitro fluorometry given by Strickland and Parsons (1968), and chlorophyll values were converted to carbon using a carbon-to-chlorophyll ratio of 57.8, determined during this study (Fig. 2).

Grazing by the copepod community was calculated by summing individual rates. The grazing rate of an individual copepod was calculated by entering the food concentration into the ingestion equation appropriate for the size of the copepod. The ingestion per individual was multiplied by the density of individuals at the depth to yield the grazing impact of that organism. This process was repeated for each of the 13 grazer organisms and summation yielded the community ingestion rate at the depth (mg C·m^{-3}·d^{-1}). This entire process was then repeated at the next depth interval with an available food concentration. After community ingestion rates were computed for all depth intervals, an integration yielded the community grazing rate for the entire water column (mg C·m^{-2}·d^{-1}).

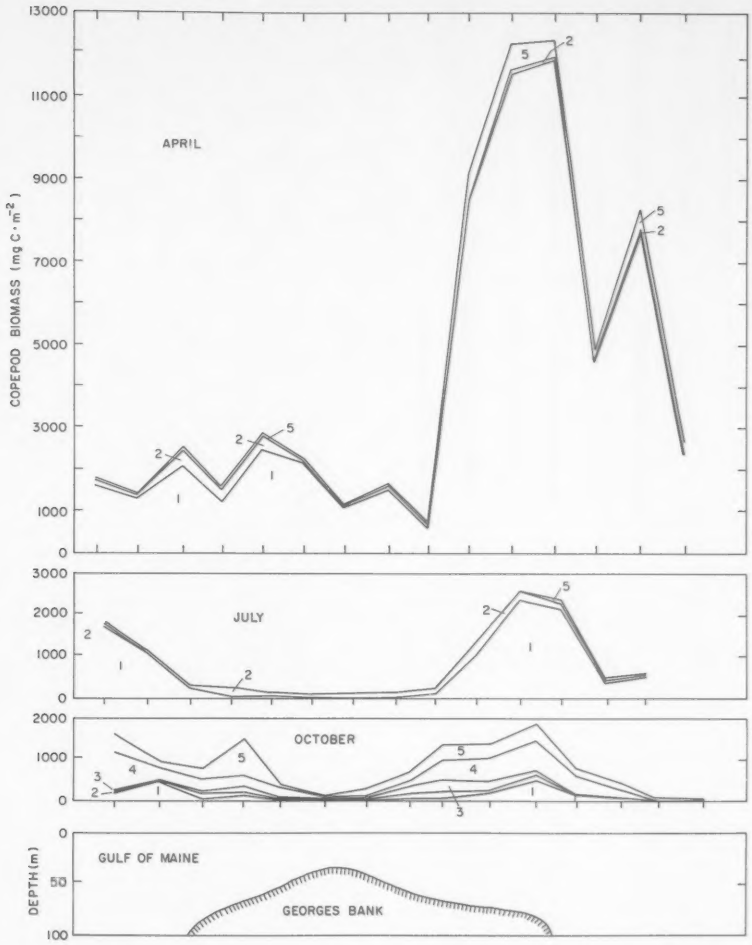

FIG. 4. Biomass of grazing copepods on the Georges Bank transect (numbers as in Fig. 3).

Results

The body size (Table 1) and numerical abundance of each grazer were combined to calculate the biomass at each station (Fig. 3 and 4). Copepodids and adults of each species are combined in the figures but separate categories are maintained in the grazing calculations. Biomass varied seasonally and spatially in both regions and there was a pronounced change in the species composition, from the *Calanus–Pseudocalanus* dominated system in April and July to the *Centropages–Oithona* dominated system in October. On the Long Island shelf, the *Calanus–Pseudocalanus* system appeared to develop between April and July whereas over Georges Bank the biomass declined over the same period. The copepod biomass was about the same in both regions during October, the period of *Centropages–Oithona* dominance. During October zooplankton were concentrated in the upper 25 m at the Long Island station whereas they were homogenously distributed at the Georges Bank station (Fig. 5). No diel migrations were apparent.

Food concentrations (Fig. 6) were generally highest in both regions during April. In July, there were high concentrations at specific locations, but many areas contained little particulate material. During October, concentrations were very low over almost the entire study area and only directly over Georges Bank were concentrations found that were >2.0 mm$^3 \cdot$L^{-1}. Chlorophyll concentrations at the pump stations (Fig. 7) showed little vertical structure in either location.

In April, grazing/m^3 by the copepod community was quite uniform over the Long Island shelf (Fig. 8). Integrated values ranged from 65 to 407 mg C$\cdot$m$^{-2}\cdot$d^{-1} ($\bar{X} = 226$) and gener-

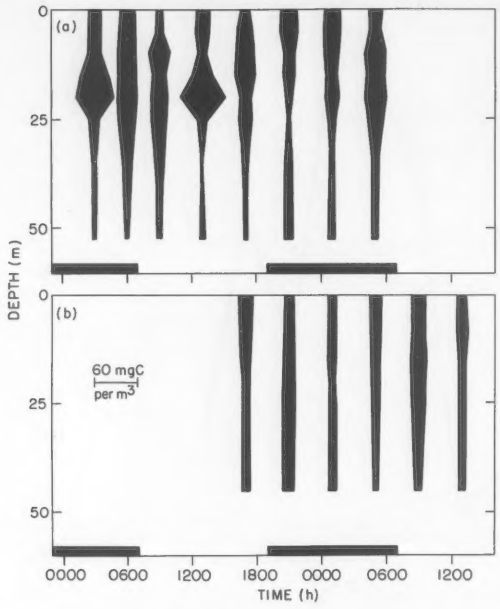

FIG. 5. Vertical distribution of grazer biomass, measured with the zooplankton pumping system, at the time–series station on the Long Island shelf (a) and on Georges Bank (b). Horizontal black bars represent hours of darkness.

ally were highest in the outer half of the shelf and over the slope. Primary production at this time averaged 817 mg $C \cdot m^{-2} \cdot d^{-1}$ (Table 2), approximately double the highest integrated grazing rate. At primary productivity stations ingestion was equivalent to 15% (nearshore) and 30% (offshore) of daily production. Over Georges Bank in April (Fig. 9), grazing/m^3 was variable, ranging from <5 to >25 mg $C \cdot m^{-3} \cdot d^{-1}$. Integrated rates were higher than on the Long Island shelf, ranging from 196 to 2003 mg $C \cdot m^{-2} \cdot d^{-1}$ ($\bar{X}$ = 770). But primary production was also high ($\bar{X}$ = 2533 mg $C \cdot m^{-2} \cdot d^{-1}$) and was never exceeded by community ingestion. At productivity stations community ingestion was equivalent to 40% (near the Gulf of Maine) and 48% (mid-Bank) of the daily primary production. The high grazing rates over the outer shelf and slope regions in both areas can be attributed to the large populations of *C. finmarchicus*, a species which requires deep water to complete its life cycle and which is not common in shallower waters.

In July on the Long Island transect, grazing/m^3 was generally higher and more variable than in April (Fig. 8); a maximum rate of >17 mg $C \cdot m^{-3} \cdot d^{-1}$ was calculated at the surface above the 70-m isobath. Integrated grazing rates ranged from 46 to 667 ($\bar{X}$ = 298) mg $C \cdot m^{-2} \cdot d^{-1}$ and never exceeded the average primary production (975 mg $C \cdot m^{-2} \cdot d^{-1}$, Table 2). At productivity stations the grazed fraction was 35% (nearshore) and 63% (outer shelf) of daily primary production. Over Georges Bank (Fig. 9), community grazing was very low in July. A maximum of about 5 mg $C \cdot m^{-3} \cdot d^{-1}$ was calculated on the outer Bank. Much of the region had community grazing rates <1 mg $C \cdot m^{-3} \cdot d^{-1}$ and integrated values were almost all <100 mg $C \cdot m^{2} \cdot d^{-1}$ ($\bar{X}$ = 79, range = 28–231). Such low grazing rates accounted for little of the daily primary production. The average grazing rate over Georges Bank in July was an order of magnitude lower than in April (79 vs. 770 mg $C \cdot m^{-2} \cdot d^{-1}$), while on the Long Island shelf grazing remained about the same or increased slightly (average values were 226 and 298 mg $C \cdot m^{-2} \cdot d^{-1}$ for April and July).

During October grazing rates on the Long Island transect were highest (43 mg $C \cdot m^{-3} \cdot d^{-1}$) nearshore, high (>21 mg $C \cdot m^{-3} \cdot d^{-1}$) in the mid-shelf area, and low (<5 mg $C \cdot m^{-3} \cdot d^{-1}$) over much of the outer half of the shelf (Fig. 8). Integrated values ranged from 31 to 711 mg $C \cdot m^{-2} \cdot d^{-1}$ and often exceeded the average primary production of 185 mg $C \cdot m^{-2} \cdot d^{-1}$ (Table 2). At primary productivity stations community ingestion was equivalent to 130% (nearshore) and 118% (outer shelf) of the daily primary production. In October over Georges Bank there were two regions with high grazing rates (>13 mg $C \cdot m^{-3} \cdot d^{-1}$) separated by a zone of low rates (<5 mg $C \cdot m^{-3} \cdot d^{-1}$) in the mid-Bank region (Fig. 9). Integrated rates reflect these patterns, and range from 20 to 859 mg $C \cdot m^{-2} \cdot d^{-1}$ ($\bar{X}$ = 289). Average primary production (770 mg $C \cdot m^{-2} \cdot d^{-1}$, Table 2) was exceeded by community grazing at only one station. At the productivity station over the Bank grazing equalled 42% of the 817 mg $C \cdot m^{-2} \cdot d^{-1}$ produced.

The vertical distribution of grazing rate is in part dependent on the vertical distribution of copepods. At the Long Island pump station, calculations using the known vertical distributions of copepods result in a grazing profile quite different from that obtained by assuming a homogenous zooplankton distribution, whereas on Georges Bank, the two profiles are similar (Fig. 10). However, integrated grazing rates were little affected by this refinement. At the Long Island station, community grazing was 212 mg $C \cdot m^{-2} \cdot d^{-1}$ for the vertically structured community and 199 mg $C \cdot m^{-2} \cdot d^{-1}$ for the theoretically homogenous community. These values were equal to 118% and 111% of the daily primary production. At the Georges Bank station, integrated ingestion rates were 386 mg $C \cdot m^{-2} \cdot d^{-1}$ for the structured community and 424 mg $C \cdot m^{-2} \cdot d^{-1}$ for the theoretically homogenous community (82% and 90% of the primary production).

Discussion

Of the three components in the calculation of community grazing rate (food concentration, grazer behavior, and grazer abundance), estimates of food concentration probably involve the most uncertainty (Longhurst 1976). In the natural environment only a portion of the total size range of particulate material is ingested by a given grazer and any measurement such as total particulate carbon, nitrogen, or chlorophyll, which characterizes the entire spectrum of particles, overestimates the food concentration. Furthermore the fraction of the particulate material ingested differs with the species and development stage of grazer, and the nutrient quality of any particle cannot be characterized by its size alone. At most

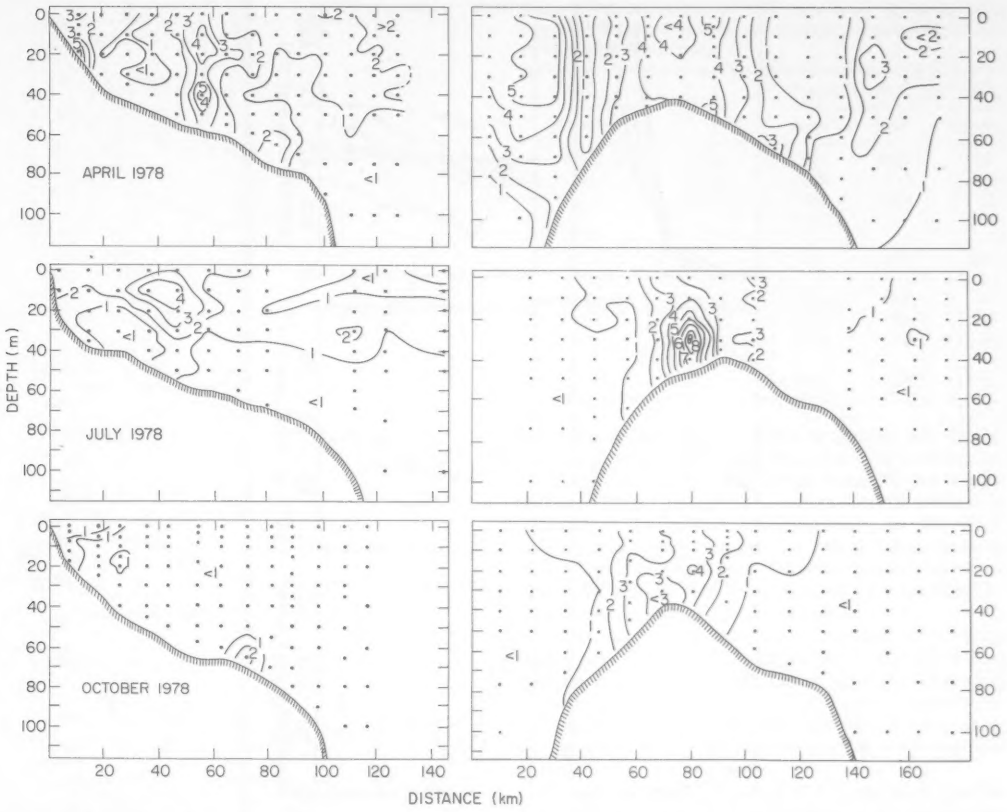

FIG. 6. Total concentration ($mm^3 \cdot L^{-1}$) of particulate material between 5 and 128 μm ESD on the Long Island transect (left) and the Georges Bank transect (right).

stations in this study, we estimated food concentration by converting the particulate material between 5 and 128 μm ESD to carbon, using an equation (Mullin et al. 1966) which takes into consideration the proportionality of cell volume to cell carbon. Although this is better than using a single conversion factor, it assumes that all the particulate material is phytoplankton. At the two pump stations, food concentrations were estimated from chlorophyll concentrations and a carbon-to-chlorophyll relationship. Where comparisons were possible, this method yielded values similar to estimates based on particulate volume.

Grazer behavior is simplified in this study so that it can be expressed as a function of food concentration and body size. Other factors of probable importance that are not incorporated into our grazing calculations include food quality, temperature, and species effects (e.g. Vidal 1980; Frost 1980). The effects of food quality on copepod feeding behavior are not well known and would be difficult to apply to the ocean. Temperature varies from 15 to 18°C over the year on the Long Island shelf surface (Walsh et al. 1978), and over Georges Bank a range of 10–12°C (Bigelow 1927) is encountered. However, few grazers encounter these temperature ranges because subsurface changes are less, and because the dominant species change seasonally as temperatures change. Probably the wide temperature ranges in the New York Bight and Georges Bank regions are less important than would be expected from laboratory studies with one copepod species. The grazing behavior of each copepod species in this study is assumed to be proportional to its size. This simplification may have led to overestimates of grazing rate for some species and underestimates for others but we did not have sufficient data to derive a separate grazing equation for each species.

Mayzaud and Poulet (1978) have suggested that copepod ingestion in the natural environment is linearly related to food concentration rather than rectilinearly, as in many laboratory studies (e.g. Frost 1972) and some field studies (O'Connors et al. 1980). If linear relationships between ingestion and food concentration had been used in this study, the calculated community grazing would not have increased greatly because food concentrations were usually insufficient to saturate the

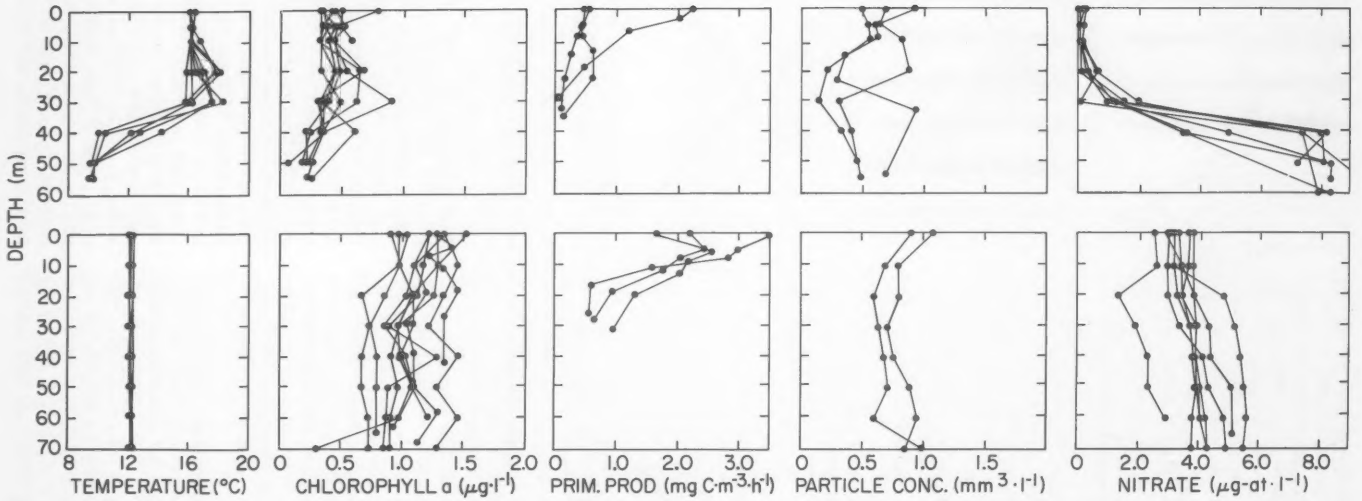

FIG. 7. Vertical distribution of temperature, chlorophyll, primary production, particulate material, and nitrate at the time–series station on the Long Island shelf (upper) and on Georges Bank (lower) in October.

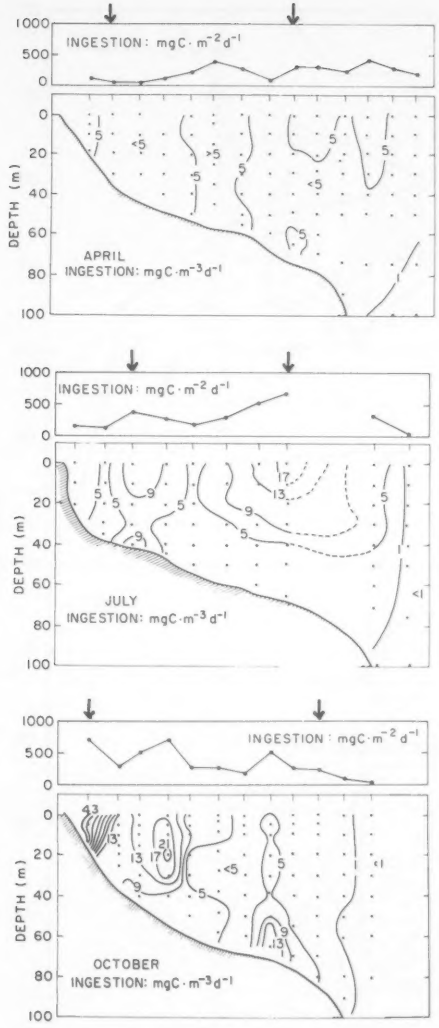

FIG. 8. Consumption rates of particulate carbon by grazing copepods on the Long Island transect. Arrows indicate primary production stations.

ingestion processes of all the copepods comprising the grazing community. At only 2 of 81 stations were all grazers feeding at maximum rates throughout the water column, and at 13 of 81 stations no grazer could feed at maximum rates anywhere in the water column. The remaining stations varied between the two extremes; somewhere in the water column food concentration was sufficient for maximum ingestion rates by small animals but rarely sufficient to saturate the feeding of large grazers.

When grazer abundance is estimated by vertical net hauls, distributional heterogeneities must be ignored. The significance of this was tested at the two pump stations during the October cruise. Incorporation of the vertical distribution of copepods into the calculation altered the vertical distribution of grazing on the Long Island shelf but not in the well-mixed Georges Bank region. However, in both regions community grazing rate, integrated over the water column, remained essentially identical with the result obtained when homogenous copepod distributions were assumed.

TABLE 2. Primary production (^{14}C) rates measured during April, July, and October, 1978, on or nearby the cruise transects (data kindly provided by P. Falkowski).

Location		Production (mg C·m^{-2}·d^{-1}) April	July	October
Long Island Shelf	Inner	424	1088	601
	Outer	1018	813	176
	Other	643	1023	92
		1182		272
	$\bar{X}$	817	975	285
Georges Bank	Inner	3694	892	
	Mid	1496	968	817
	Other	2408	388	723
	$\bar{X}$	2533	749	770

In our study, the community grazing rate often varied widely over short distances. This is not surprising because both phytoplankton and zooplankton were heterogeneously distributed. If more variables (e.g. food quality, temperature, and species effects) were incorporated into the calculation, the variability in the computed grazing rate would probably increase.

On the Long Island shelf, much of the spring phytoplankton bloom was not grazed. This was particularly true for the inner shelf, an area inaccessible to the large population of *Calanus* that develops in deeper waters. Over Georges Bank, community grazing rates in April were much higher than on the Long Island shelf but primary production was also higher so the fraction grazed was about the same in both regions.

In July over Georges Bank food was plentiful but grazer abundance was so low that community grazing averaged only about 10% of the daily primary production. Perhaps predators had cropped the zooplankton or perhaps the *Calanus* population had developed to overwintering stages and descended to deeper waters.

By the fall both regions had changed from a *Calanus–Pseudocalanus* to a *Centropages–Oithona* dominated system. All of the small amount of daily primary production over the Long Island shelf, and a large proportion over Georges Bank, was grazed. Either the change in species composition resulted in a more complete utilization of the phytoplankton or the autumn grazing rates are overestimated relative to those for the other two cruises. The large populations of *Oithona*, an inefficient grazer (Poulet 1978) which therefore may not be well represented by the Mullin and Brooks equations, could cause this discrepancy.

In other locations the fraction of phytoplankton production

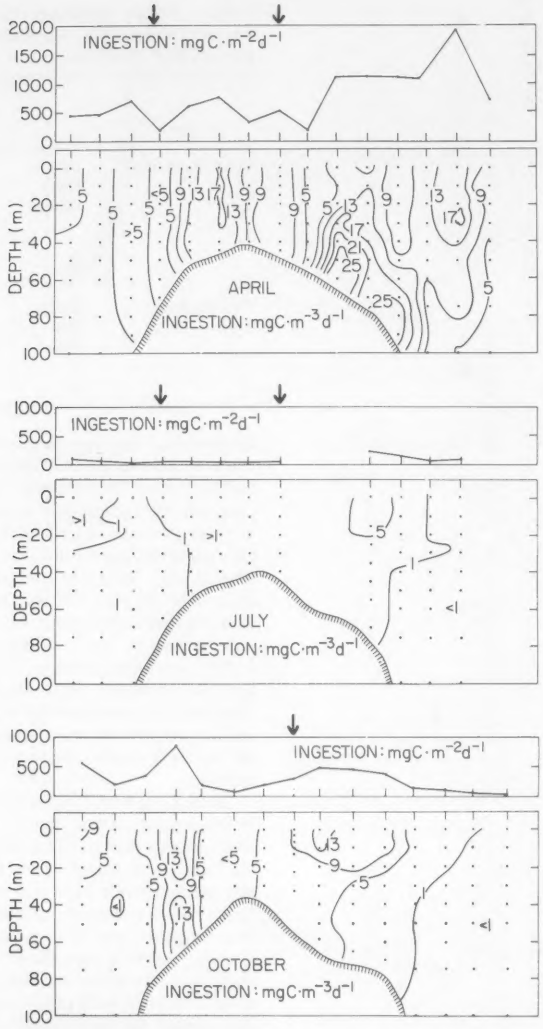

FIG. 9. Consumption rates of particulate carbon by grazing copepods on the Georges Bank transect. Arrows indicate primary production stations.

that is grazed ranges widely. In their model of Narragansett Bay, Kremer and Nixon (1978) estimated that between 31 and 82% of the annual net primary production was consumed by copepods, with an average value for their eight stations of 62%. Conversely in a eutrophic Japanese Bay, Taguchi and Fukuchi (1975) indicated that losses due to grazing ranged from 0.1 to 1.0% during the spring bloom. McAllister (1972) at station "P" in the subarctic Pacific Ocean estimated that an average of 40% of the annual primary production was ingested by the measured stock of zooplankton, with values ranging from 16 to 54% over the 6 yr reported in his study. In the Hudson River Plume about 10% of the phytoplankton production was ingested in April, about 26% in July, and about 7% in October (Malone and Chervin 1979). The authors suggested that most of the diatom production occurring before thermal stratification each year is not grazed whereas most of the summer, nanoplankton production is grazed. Riley and Bumpus (1946) suggested a grazing rate of 6.4% of the phytoplankton population per day for Georges Bank in April, approximately equivalent to 670 mg $C \cdot m^{-2} \cdot d^{-1}$. This compares favorably to our average value of 770 mg $C \cdot m^{-2} \cdot d^{-1}$ for Georges Bank in April.

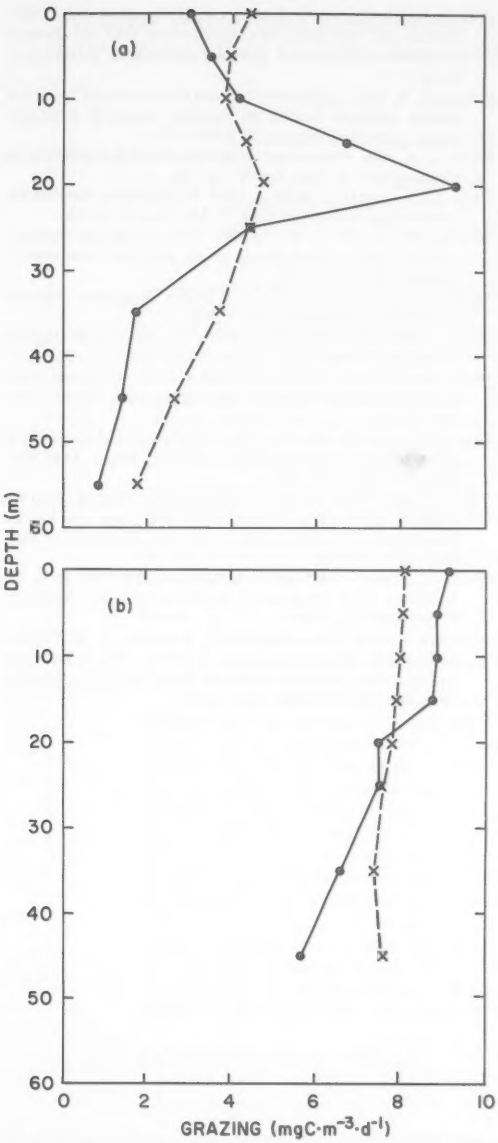

FIG. 10. Vertical distribution of community grazing at the time-series station on the Long Island shelf (a) and on Georges Bank (b): (●—●), grazing calculated with discrete estimates of copepod abundance; (×---×), grazing calculated with discrete estimates of zooplankton abundance averaged to produce a situation analogous to a vertical net haul.

A summary of our calculations suggests that of the ~250 g $C \cdot m^{-2} \cdot yr^{-1}$ produced by the phytoplankton over the Long Island shelf (P. Falkowski, Brookhaven Lab, Upton, NY 11973, personal communication), about 115 g are not grazed by the net-caught copepod community, and of the ~375 g $C \cdot m^{-2} \cdot yr^{-1}$ produced over Georges Bank (Cohen et al. 1982), about 200 g are not grazed. Thus we estimate that about 50% of the annual particulate primary production of both regions is grazed by the copepod community, with the greatest uncoupling occurring during the spring bloom. This agrees with the conclusions of Riley (1946) that no single factor completely controls the phytoplankton crop and suggests that a significant fraction of the annual phytoplankton production in these regions either sinks to the benthos or is exported via advective processes.

Acknowledgments

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Coastal Water Mass Replacement: Its Effect on Zooplankton Dynamics and the Predator–Prey Complex Associated with Larval Capelin (*Mallotus villosus*)[1]

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FRANK, K. T., AND W. C. LEGGETT. 1982. Coastal water mass replacement: its effect on zooplankton dynamics and the predator–prey complex associated with larval capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 39: 991–1003.

We examined the hypothesis that the onshore wind-regulated initiation of larval emergence and drift in capelin (*Mallotus villosus*) was adaptive. Onshore winds were found to induce rapid water mass exchange in coastal Newfoundland resulting in the replacement of cold, high-saline, predator-laden waters with warmer, less-saline waters in which the abundance of an important fraction of the predator community was reduced 3- to 20-fold and zooplankton densities in the edible size fraction were increased 2- to 3-fold. In situ enclosure experiments indicate that the synchronous emergence of larval capelin during onshore winds, coupled with the reduced predator density at this time, results in predator satiation. Wind-induced elevations of the biomass of the edible zooplankton size fraction can produce fivefold increases in the daily growth rate of larval capelin. Capelin larvae thus initiate their drift and first feeding in a wind-induced "safe site." The abundance of eggs and larvae of 11 other marine fish species were also found to be associated with this "safe site" water mass.

Key words: capelin, *Mallotus villosus*; water mass replacement, predation, feeding, growth, larval fish, survival, wind effects, drift, dispersal, enclosures, zooplankton

FRANK, K. T., AND W. C. LEGGETT. 1982. Coastal water mass replacement: its effect on zooplankton dynamics and the predator–prey complex associated with larval capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 39: 991–1003.

Nous avons étudié l'hypothèse selon laquelle le début de l'émergence des larves de capelan (*Mallotus villosus*) et de leur dérive occasionnées par le vent du large est adaptatif. Nous avons découvert que les vents du large provoquaient un échange rapide de la masse d'eau sur les côtes de Terre-Neuve, donnant lieu au remplacement des eaux froides de forte salinité et remplies de prédateurs par des eaux plus chaudes et moins salines. Dans celles-ci, l'abondance d'une fraction importante de la communauté de prédateurs était réduite de 3 à 20 fois, et la densité du zooplancton composant la fraction de grosseur comestible était accrue de 2 à 3 fois. Des expériences de mise en captivité in situ ont démontré que l'émergence synchrone du capelan larvaire au moment des vents du large, de paire avec une densité réduite des prédateurs à ce moment, mènent à l'assouvissement du prédateur. Les augmentations de la biomasse de la fraction de zooplancton de taille comestible provoquées par le vent peuvent quintupler le taux de croissance quotidienne du capelan larvaire, qui débute ainsi sa dérive et sa première alimentation dans un endroit rendu sûr par le vente. Nous avons en outre découvert que l'abondance des œufs et des larves de 11 autres espèces de poissons marins était également plus grande dans cet endroit sûr de la masse d'eau.

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MOST marine fish species which reproduce in coastal systems rely on turbulent and horizontal water flow for the dispersal of their offspring (see review in Johannes 1978; Frank and Leggett 1981). The extent to which this transport results in the larvae being carried to areas where conditions are favorable for survival ("safe sites" Harper et al. 1961) has long been considered a major regulator of the population dynamics of marine larval fishes (Ketchen 1956; Stevenson 1962; Martin and Kohler 1965; Nelson et al. 1977). The ultimate determinants of early larval survival and hence the primary features of "safe sites" are widely held to be food conditions (see Cushing 1975; Ware 1977) and predator abundance (Hempel 1965; Cushing 1969; Ware 1975, 1980). Documenting the existence of "safe sites" and the physical processes which produce them, quantifying their role in the regulation of larval survival, and clearly establishing an adaptive relationship

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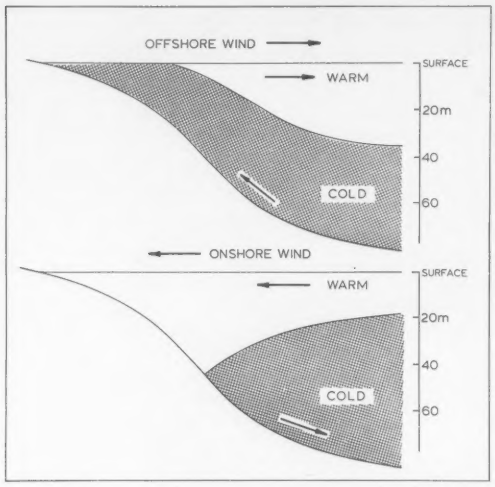

FIG. 1. Schematic representation of the effect of offshore and onshore winds on the summer water temperatures and water layers in the nearshore zone along Newfoundland's east coast (redrawn from Templeman 1966, fig. 27).

between reproductive behavior, transport processes, and the occurrence of "safe sites" has, however, proved very difficult in most instances.

In this paper we examine the role of physical factors in the regulation of early larval transport in capelin (*Mallotus villosus*), and the structure of the predator–prey community to which they are exposed during drift. Our working hypothesis was that factors regulating the onset and direction of larval drift would also produce favorable feeding conditions and minimize predator abundance. Inherent in the formulation of this hypothesis is the assumption that the timing of the initiation of larval drift in capelin is adaptive.

Capelin is a dominant element in the Northwest Atlantic food web (Bailey et al. 1977). In the Northwest Atlantic the major beach-spawning areas are located on the east coast of Newfoundland and Labrador. Spawning sites are typically exposed beaches located at the heads of long embayments (Templeman 1948). The adhesive eggs cling to coarse-grained intertidal sediments, wave and tidal action serving to bury the eggs approximately uniformly over the top 20 cm of the beach gravel between the low and high tide zones. Larvae hatch in the beach gravel which they exit not gradually, but as highly concentrated patches predictably linked to the occurrence of onshore winds (Frank and Leggett 1981). The timing of the dispersal event is unpredictable and its frequency low, the summer winds in eastern Newfoundland and Labrador being predominately offshore (Frank and Leggett 1981, Fig. 2). Larval capelin thus initiate their drift, and first feeding, in an environment that is transitory, predictable with respect to wind conditions, and consistent over the species range in Newfoundland (Frank and Leggett 1981). Lambert et al. (1982) have recently confirmed this fact for capelin spawning in St. Georges Bay, N.S. Equally important from the point of view of the study of capelin, the early phase of development occurs onshore where it can be easily and economically investigated.

With respect to the structure of the environment during early larval drift, it is well known that coastal water mass replacement can occur quickly as a result of changes in wind speed and direction. This often results in pronounced changes in temperature and salinity (Sverdrup 1938; Hachey 1955; Taylor and Stewart 1959; Cooper 1960). The character of the planktonic community is also altered during periods of water mass replacement, the origin of a given water mass being frequently traceable by the occurrence of "indicator species" (see reviews in Russell 1952; Alvariño 1965).

Returning to our hypothesis, as a test of the "safe site" concept, we predicted a priori that the initiation of larval drift and first feeding in larval capelin would occur in an environment characterized by high densities of zooplankton in the edible size spectra and low densities of the major predators (i.e. that the time of drift and first feeding would be strongly matched to the existence of favorable predator–prey abundances). We predicted further, that changes in prey and predator densities would be strongly linked to wind conditions which is, also, a key factor regulating the initiation of drift (Frank and Leggett 1981).

Water Mass Replacement

GENERAL

The summer waters off Newfoundland's east coast are characterized by a shallow (~30 m thick) warm upper layer and a deeper cold layer extending from the base of the warm layer to the bottom (~180 m) (Templeman and Fleming 1963). Templeman (1966) suggested that the wind, operating on the warm surface layer, may significantly influence the thermal and biological characteristics of nearshore waters. He hypothesized that offshore winds may blow the less-dense, warm surface water offshore causing the heavier, colder bottom water to move shoreward and replace it. Onshore winds, in contrast, would cause warmer surface water to predominate along the coast (Fig. 1). Assuming water mass replacement occurs, the nearshore waters off eastern Newfoundland and Labrador should be dominated by waters whose origin is the deeper, colder, more saline layer as offshore winds predominate during June, July, and August. For example, monthly meteorological summaries for St. John's–Torbay, published by Environment Canada, show the average number of days during which offshore winds prevailed to be 24.1 (SD 2.9) and 26.8 (SD 3.0) in June and July, respectively, over the 21-yr period 1960–80 (see also Fig. 2). The occurrence of warmer, less-saline surface waters in the nearshore region would be restricted to the occasional and unpredictable occurrence of onshore winds. If water mass replacement does occur as a result of wind effects, capelin larvae would consistently be released into an environment dominated by the warmer, less-saline surface water mass and its associated biota.

TEMPERATURE

To evaluate Templeman's (1966) hypothesis concerning wind-induced water mass replacement we examined the relationship between nearshore water temperature and wind

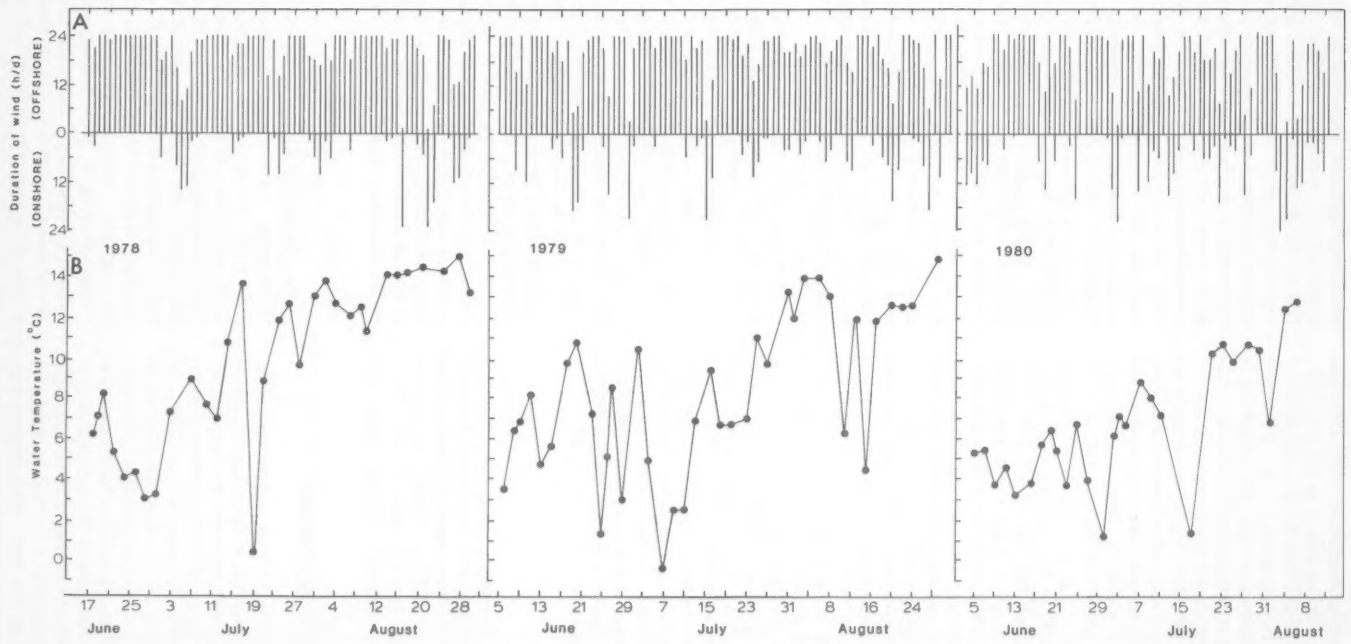

FIG. 2. (A) Daily duration of offshore (SE–NW) and onshore (N–E) wind (lines above and below the zero line, respectively) during June–August (1978, 1979, 1980). This data was obtained from the Holyrood (Newfoundland Hydro) meteorological station located 30 km south of the study site. (B) Mean water temperatures in the 1- to 2-m-depth strata at the Bryant's Cove study site. Note the quick change in water temperature in response to changes in wind direction.

events. We measured water temperatures in 1978, 1979, and 1980 at six hydrographic stations located at 15-, 60-, 120-, 215-, 490-, and 730-m distances from the spawning beach in Bryant's Cove. Stations were occupied at 1- to 3-d intervals and temperature measurements were made at 1-m-depth intervals (surface to bottom) using a Hydrolab FT-3 marine hydrographic thermometer. Water depths at the respective stations proceeding seaward were 3 m, 5 m, 7 m, 10 m, 16 m, 22 m. Horizontal (between station) and vertical temperature differences were slight and nonsystematic during both onshore and offshore wind conditions during the June–August study period (1978: offshore, $\Delta H = 0.6$, $\Delta V = 1.1$°C, $n = 17$; onshore, $\Delta H = 0.3$, $\Delta V = 0.8$, $n = 15$; 1979: offshore, $\Delta H = 0.9$, $\Delta V = 2.0$, $n = 19$; onshore, $\Delta H = 0.7$, $\Delta V = 1.6$, $n = 19$; 1980: offshore, $\Delta H = 0.8$, $\Delta V = 2.5$, $n = 9$; onshore, $\Delta H = 0.6$, $\Delta V = 3.2$, $n = 19$). These findings indicate that the nearshore waters are well mixed under both wind conditions. Dramatic short-term changes in water temperature were frequent and were consistently associated with changes in wind direction (Fig. 2). Daily deviations from the monthly mean temperatures at the 1- to 2-m-depth strata were nonsystematic with respect to time, but strongly correlated to wind events ($\chi^2 = 25.8$, df = 2, $P < 0.001$). Eighty-five percent of the negative deviations in excess of 1°C were associated with offshore wind (SE through NW) and 81% of the positive deviations in excess of 1°C were associated with onshore winds (N through E). Exceptions to this general pattern occurred only when winds were light (<20 km/h). These observations are consistent with Templeman's water mass exchange hypothesis. Deep, cold waters appear to replace warmer surface waters in the inshore areas when winds are offshore. Onshore winds reverse this condition. The rate of change in nearshore temperatures following changes in wind direction (Fig. 2) suggest that the water mass replacement is rapid.

Salinity

Salinity at the 1- to 2-m-depth strata was determined at weekly intervals coincident with temperature measurements in 1979. Nearshore salinities were significantly higher during offshore (mean = 32.32‰) relative to onshore (mean = 31.67‰) winds ($t = 3.5$, df = 9, $P < 0.01$). These findings are also consistent with the water mass replacement hypothesis.

Predator–Prey Dynamics

To examine the effect of water mass replacement on the dynamics of the potential predators of larval capelin, and on the biomass of the edible zooplankton size fraction available to larval capelin as prey, we sampled the nearshore plankton community at 1- to 3-d intervals during 1979 and 1980. All samples were collected with a 0.5-m-diameter plankton net fitted with a No. 10 (150 μm) mesh net and General Oceanics flowmeter. During the initial stages of larval drift capelin are transported as passive contaminants (Fortier and Leggett 1982) and are therefore subject to extensive vertical mixing in the nearshore area. All collections were made by towing the net horizontally in the 1- to 2-m-depth strata along six transects parallel to and at increasing distances from the beach. Each sampling transect spanned the width of the cove and intersected the positions of the fixed hydrographic stations. Towing speeds averaged 1.2 ± 0.07 m/s. All samples were collected between 18:00 and 20:00 and were preserved in 4% buffered formalin. Five components of the macrozooplankton, known by previous work to be important predators on fish larvae, were sorted and counted. They were chaetognaths (identified as voracious predators on larval fish by Lebour 1922, 1923; Bigelow 1926; Thomson 1947; David 1955; Furnestin 1957; Stevenson 1962), jellyfish (confirmed as predators by Russell 1953; Stevenson 1962; Fraser 1969; Phillips et al. 1969; Larson 1976; Möller 1980), ctenophores (shown to be important predators by Lebour 1922, 1923; Bigelow 1926; Russell 1935a; Fraser 1962; Stevenson 1962; Fraser 1970), decapod larvae and amphipods (identified as important predators by Lebour 1925; Rosenthal 1967; Lillelund and Lasker 1971; Theilacker and Lasker 1974; von Westernhagen and Rosenthal 1976). The most common members of each group were chaetognaths — *Sagitta elegans*; jellyfish — *Sarsia tubulosa*, *S. princeps*, *Catablema vesicarium*, *Aglantha digitale*, *Leukaritiara nobilis*, *Euphysa flammea*, *Aurelia* sp., *Cyanea* sp.; ctenophores — *Pleurobrachia* sp.; decapod larvae — crab zoea of Majidae; amphipods — primarily hyperiids. Predator densities were recorded as no./m^3 of water filtered.

The balance of the plankton sample, the bulk of which was planktonic crustaceans (primarily *Calanus finmarchicus* and euphausids of a variety of developmental stages and appendicularians *Oikopleura* sp.), was fractionated into the edible (<250 μm) and inedible (>250 μm) size fractions. We washed each sample through a 250-μm sieve. Both fractions were rinsed with freshwater, resuspended, and filtered through a preweighed glass microfiber filter by aspiration. The filters were placed in a drying oven at 70°C for 24 h, removed to a desiccator, and weighed to an accuracy of 10 μg. The dry weight biomass of each size fraction was determined by difference. All dry weight determinations were expressed as μg/m^3. All prey and predator density data were log ($y + 1$) transformed prior to analysis because the untransformed data exhibited a tendency for the variance to be positively correlated to the mean. This transformation effectively stabilized the variance. Wind data (expressed as hours of onshore wind·d^{-1}/24) was arcsine transformed to normalize the distribution (Sokal and Rohlf 1969).

Predators

The absolute abundance of jellyfish, ctenophores, and chaetognaths showed no significant temporal pattern ($r^2 < 0.04$). Decapod and amphipod abundance showed weak correlations with time but were opposite in sign between years. Abundances of jellyfish and chaetognaths were, however, significantly negatively correlated with the daily duration of onshore winds (for the day of, and the day prior to, sampling) in both 1979 and 1980. The sign of this relationship was consistent both between years and between stations within years (Fig. 3). These findings suggest their presence is linked to the upwelling of the deeper, more saline waters. This interpretation is consistent with the known depth distribution of these organisms. The summer depth distribution of chaetognaths is reported to be in the 40- to 100-m range with very

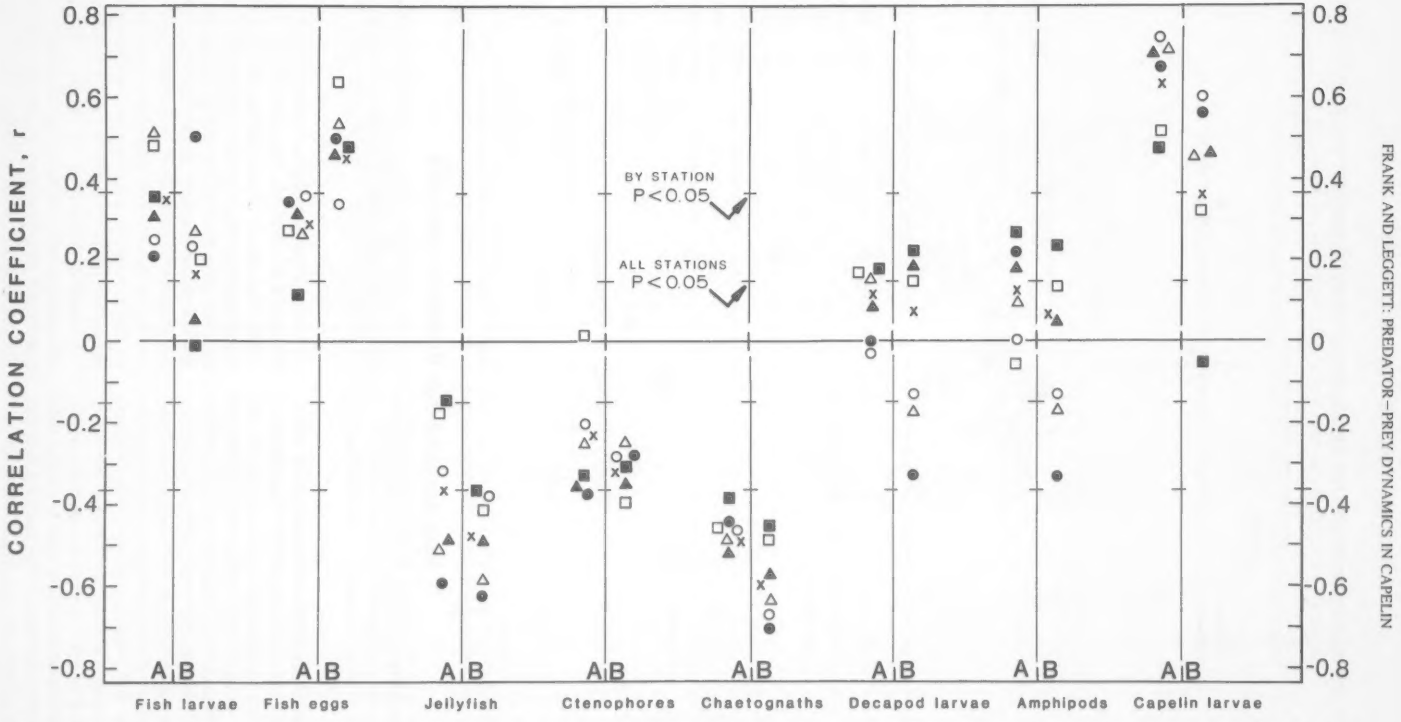

FIG. 3. Plot of the correlation coefficients resulting from the regression of macrozooplankton density (no./m^3) on the daily % duration of onshore wind at each station (○, 15 m; ●, 60 m; △, 120 m; ▲, 215 m; □, 490 m; ■, 730 m; ×, all stations). (A) 1979, (B) 1980.

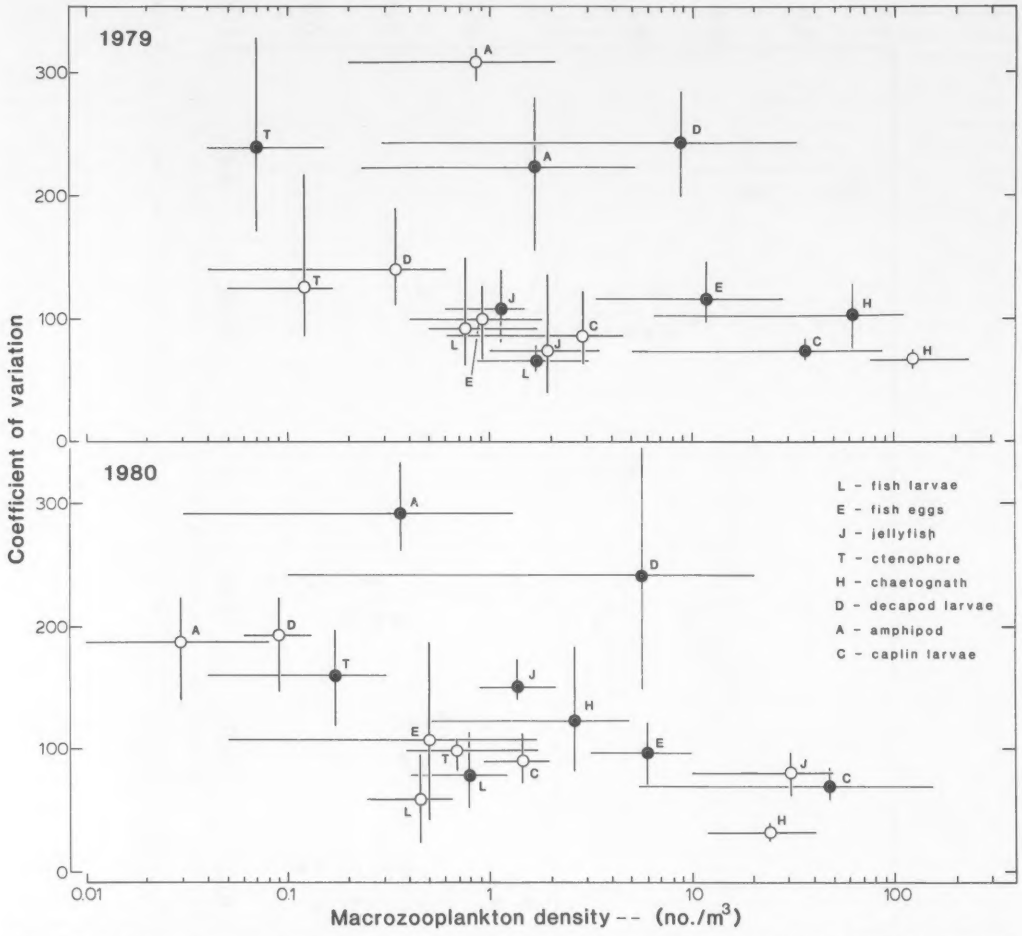

FIG. 4. Plot of the mean summer density (no./m³) of each macrozooplankton component ($\text{Mean}_{\text{cove}}$ = Σ station means/no. of stations) against the mean coefficient of variation ($\overline{CV}$ = Σ station CVs/no. of stations) during onshore (●) and offshore (○) wind conditions for 1979 and 1980 (upper and lower panel, respectively). Horizontal and vertical lines indicate the range of station means and CVs, respectively.

few occurring near the surface (Huntsman and Reid 1921; Bigelow 1926; Russell 1933; Alvariño 1965). The center of distribution of jellyfish is reported to be in the 50- to 150-m-depth range, strongly overlapping that of chaetognaths (Mayer 1910; Kramp 1913b; Kramp and Damas 1925; Bigelow 1926). Both jellyfish and chaetognaths have previously been reported to exhibit pronounced changes in abundance related to the influx of different water masses into the areas sampled (Meek 1928; Russell 1935a, 1935b; Maaden 1942a; Thiel 1962; Alvariño 1965; Russell 1970). Given the relatively large number of correlations presented the possibility of chance significant correlations must be considered. We believe this serendipitous effect to be minimal because of the very low probability levels associated with most correlations (jellyfish 8 of 14, $P < 0.01$; 6 of 14, $P < 0.001$. Chaetognaths 11 of 14, $P < 0.01$; 10 of 14, $P < 0.001$).

The abundances of amphipods and decapod larvae were largely independent of wind condition (Fig. 3). Both species are known to exhibit diel vertical migration and are often found in dense swarms at the surface under low light intensities (Bigelow 1926). Their association with specific water masses is thus transitory and time dependent. This would explain the absence of consistent correlations of their density with either onshore or offshore wind conditions.

Ctenophore abundance was weakly negatively correlated with onshore winds. The reported catholic behavior of ctenophores with respect to temperature and depth (Kramp 1913a; Rose 1913; Bigelow 1926; Fraser 1970) is consistent with the

TABLE 1. Hypothetical differences in the physical and biological characteristics of the surface and subsurface water masses entering into Bryant's Cove during mid-July.

Water mass properties	Wind direction		
	Onshore[a]	Offshore	Magnitude of difference
Physical			
T° water	High	Low	≥3°C
Salinity	32‰<	>32‰	0.65‰
Biological — Predator density			
Chaetognaths	Low	High	10–20 ×
Jellyfish	Low	High	3–5 ×
Decapod larvae	Same	Same	—
Ctenophores	Low	High	1.1–1.5 ×
Amphipods	Same	Same	—
Zooplankton biomass by size[b]			
Zoo. >250 μm (inedible)	Same	Same	—
Zoo. <250 μm (edible)	High	Low	2–3 ×
Density of capelin larvae	High	Low	100 ×
Effect on larval capelin			
Death due to predation	Low	High	
Expected daily growth rate	High	Low	1.2–5.5 ×

[a]Assuming average daily duration of onshore winds = 18 h.
[b]Growing degree-day value (GDD) was set at 600°C·d for these calculations.

TABLE 2. Results of stepwise regression to predict the biomass ($\log_{10}$ μg·m^{-3}, dry wt) of edible (<250 μm) and inedible (>250 μm) zooplankton from cumulative growing degree days and the daily % duration of onshore wind (arcsine transformed) (**$P < 0.01$; ***$P < 0.001$; ns, $P > 0.05$).

Zooplankton size fraction	n	Variable	Estimated coefficient[a]	Multiple R^2	Increase in R^2	$\lvert t\rvert$[b]
Edible (<250 μm)	51	GDD	0.001353	0.4529	0.4529	7.1***
		WIND	0.004511	0.5359	0.0830	2.9**
		$y_{intercept}$	3.04289	—	—	33.1***
Inedible (>250 μm)	51	GDD	0.002246	0.6178	0.6178	8.7***
		WIND	−0.001471	0.6217	0.0040	0.7 ns
		$y_{intercept}$	3.05056	—	—	24.9***

[a]The estimated coefficients and their t values are those for the final step of the regression analysis.
[b]t values were derived to test the null hypothesis that the true value of the coefficient is equal to zero.

weak nature of this correlation.

These findings are fully consistent with the water mass replacement hypothesis. The temporal coefficient of variation of ctenophores, chaetognaths, and jellyfish densities was always greatest during onshore winds (Fig. 4). This observation is also in agreement with our suggestion that inshore waters off eastern Newfoundland are dominated by the upwelling of deeper cold waters induced by the prevailing offshore winds. The duration and magnitude of the replacement of these waters, and their associated biota, by warmer surface waters is expected to be a variable function of the duration and intensity of onshore winds. Hence the higher variability of the deep-water-associated predators under onshore wind conditions.

We conclude that the density of an important fraction of the potential predator community is directly controlled by prevailing wind conditions which generate water mass replacement. Assuming an 18-h average duration of onshore winds we estimate a 3- to 5-fold decrease in the abundance of jellyfish and a 10- to 20-fold decrease in the abundance of chaetognaths relative to periods of offshore wind (Table 1).

PREY

The absolute biomass of both zooplankton size-classes in both 1979 and 1980 was positively correlated with cumulative growing degree days (GDD) beginning on April 1 (as reported in monthly meteorological summaries, St. John's–Torbay, published by Environment Canada) (Table 2). To separate this seasonal effect from the potential effect of wind on the biomass of edible and inedible zooplankton, we performed stepwise multiple regression analyses incorporating as independent variables both cumulative growing degree days (seasonal effect) and the duration of onshore wind (expressed as $\sin^{-1}$ (h onshore wind·d^{-1}/24)$^{0.5}$ for the day of, and the day prior to, sampling). The seasonal effect was then held constant and the wind effect analyzed for the direction and intensity of its impact on the two zooplankton size-classes. We

were particularly interested in the effect on the <250-μm size-class as Bjørke (1976) had shown that the diet of first feeding capelin larvae consists mainly of copepod eggs and nauplii which, in our study area, ranged in size from 132 to 155 μm for eggs and up to 300 μm for early naupliar stages.

A significant fraction of the daily variation in the absolute biomass of the edible (<250 μm) size-class was explained by the wind variable (Table 2), the biomass of this fraction being positively related to the duration of onshore winds. The biomass of the >250-μm fraction was not significantly correlated with the duration of onshore winds (Table 2). Assuming an 18-h-average duration of onshore wind we estimate an approximate 2−3× increase in the absolute biomass of the <250-μm-size fraction relative to its abundance during offshore winds (Table 1).

The positive relationship between onshore winds and the absolute biomass of the <250-μm-size fraction is consistent with the water mass replacement hypothesis as the reported depth distribution of copepod eggs and nauplii is within the upper 30-m strata, there being little tendency for the young of most planktonic crustacea to exhibit vertical migration until the later developmental stages. The absence of a significant relationship between the abundance of the >250-μm-size-class and wind events is also consistent with the hypothesis as these older, larger elements of the plankton are known to make extensive diel vertical migrations thereby associating themselves alternatively with both the deep and surface water masses (With 1915; Nicholls 1933; McLaren 1963).

Water Mass Replacement and "Safe Sites" for Capelin

We have shown that onshore winds in the eastern Newfoundland area have at least four predictable effects: they facilitate the release of capelin larvae from the beach gravel and their entry into the pelagic environment (Frank and Leggett 1981); they induce water mass changes in the nearshore water causing it to be dominated by warmer, less-saline surface waters; they cause a 3- to 20-fold reduction in the abundance of an important fraction of the potential larval capelin predator complex; and they induce a 2- to 3-fold increase in the absolute biomass of the potential food resource for larval capelin. These last two effects are directly linked to water mass replacement. The direction and approximate magnitude of these related effects are summarized in Table 1. These findings are consistent with our initial hypothesis. The timing of the entry of larval capelin into the pelagic environment to coincide with periods of onshore winds is thus interpreted to be adaptive. This conclusion is strengthened by the results of recent experiments (Frank and Leggett unpublished data) showing that the increase in water temperature associated with onshore winds is a significant stimulus to larval emergence. This increased emergence rate is independent of the role of physical disturbances of the sediments in larval release. We conclude that the emergence of larval capelin during periods of onshore winds minimizes their potential mortality due to predation and maximizes their probability of encountering abundant food resources in the appropriate size spectra at the onset of exogenous feeding.

The reciprocal patterns of predator/larval capelin densities, mediated by wind events, are illustrated in Fig. 5 which portrays a simulation of the absolute abundance of these predators, relative to larval capelin, at various distances from the spawning beach under different durations of onshore winds. These simulations are based on the analysis of the relationships between wind condition and predator density summarized in Fig. 3. We have previously shown (Frank and Leggett 1981) that the high concentration of capelin larvae in the nearshore areas during onshore wind events results from the synchronous emergence of larvae from the gravel during onshore winds and not from concentration of larvae in the nearshore area due to Ekman transport from offshore areas. The high concentrations of larvae in the nearshore area, depicted in these simulations, reflect the situation up to 1 d after the onset of onshore winds. The subsequent time course of larval distributions indicates that larvae move offshore in patches, associated with surface waters, under the influence of offshore winds (C. Taggart personal communication). The reduction in predator densities, resulting from water mass replacement, is significant over the entire nearshore area, ranging from 3- to 30-fold depending on location and wind condition.

Predator Swamping

The low predator densities during onshore winds, coupled with the pulsed, high-density entry of capelin larvae into the pelagic environment, suggests that the impact of predation may be further reduced by predator swamping. To evaluate this hypothesis we conducted a series of experiments designed to assess the effect of larval density on mortality rate due to predation. We used in situ enclosures having the following specifications: 1 m diam × 5 m deep, cylindrical, volume 4 m^3, construction nitex 150 μm, steel hoops at 1-m intervals, bottom panel tapered to cod end. Enclosures were suspended from wooden boxframe floats anchored in water 7−8 m in depth and were stocked with yolk sac larvae obtained from the beach sediments. Larval densities, which ranged from 20 to 1070/m^3, spanned the average range of larval densities observed in situ. Each enclosure was stocked with 20 ctenophores giving an initial density of 5/m^3. This initial density was 2−5 times the average density of ctenophores in the nearshore area. This high density was used to ensure that evidence of predator swamping, if obtained, was unequivocal. In addition, ctenophores are known to swarm in response to high prey concentrations (Fraser 1970), hence actual concentrations in local areas may exceed our integrated density estimates which were based on plankton tows. All ctenophores (*Pleurobrachia* sp.) were collected either by dipnetting from a boat or by SCUBA-equipped divers using slurp guns. All experiments were of 3-d duration. Each treatment was paired. Six trials were conducted in 1979 and 12 in 1980. Paired control enclosures stocked with 500 larvae but lacking predators were run in both years. At the end of each trial the enclosures were lifted, the contents retrieved from the cod end, and the number of larvae remaining assessed. Mortality unrelated to predation was assessed from the controls. Mortality due to predation in the experimental enclosures was determined as total mortality-control mortality. There was no apparent relationship between larval mortality and water temperature ($r = -0.271$, $P > 0.05$). Ctenophores were used because their densities were found to be least affected by

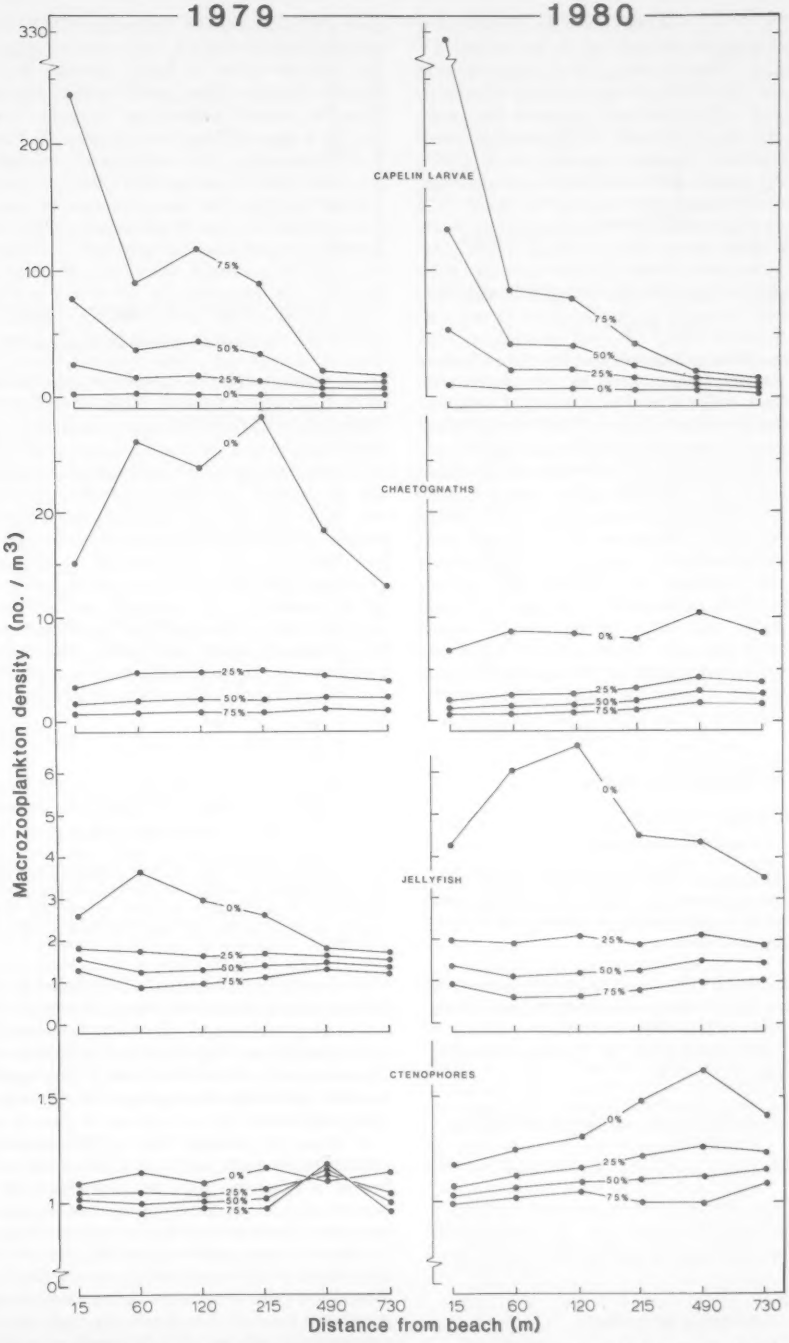

FIG. 5. Simulation of densities of larval capelin, chaetognaths, jellyfish, and ctenophores under variable durations of onshore wind for 1979 and 1980. Predictions were derived from the regression models used to construct Fig. 3.

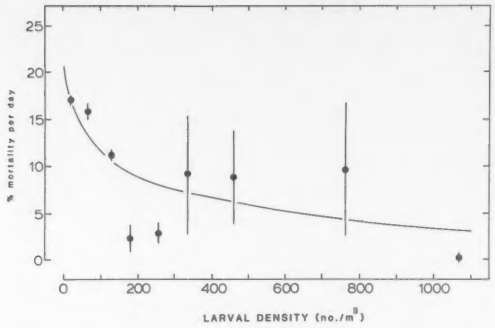

FIG. 6. Relationship between % mortality per day of capelin larvae (mean, $n = 2$) resulting from predation by ctenophores under increasing densities of capelin larvae. In situ enclosure experiments were used to develop this data set. Vertical bars show the range.

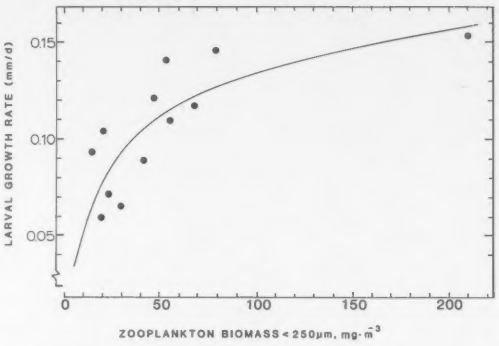

FIG. 8. Relationship between daily larval growth rate and biomass of edible (<250 µm) zooplankton determined from experiments conducted with in situ enclosures.

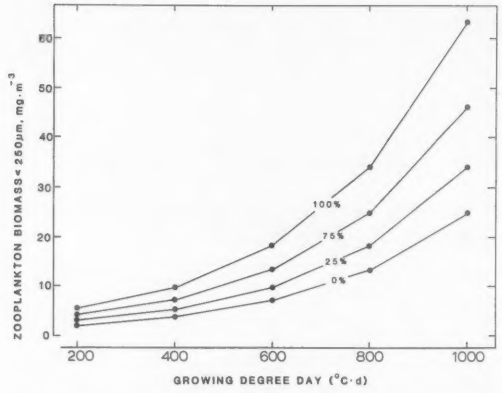

FIG. 7. Simulation of model (Table 2) which predicts the edible (<250 µm) zooplankton biomass as a function of cumulative growing degree days and the % daily duration of onshore wind (indicated by values intersecting each line).

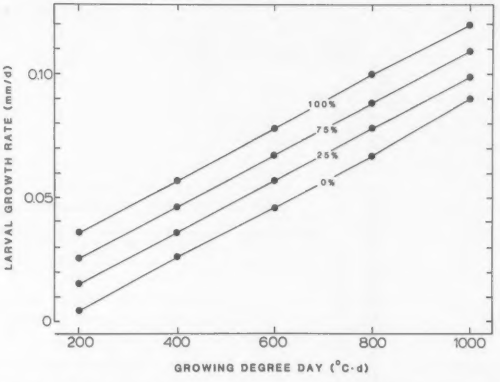

FIG. 9. Daily growth rate of larval capelin predicted from wind-induced changes in edible zooplankton biomass (see Fig. 9 and equation 2). Note elevation in larval growth rate under increasing duration of onshore wind (% values) at each growing degree day.

water mass replacement (Fig. 3, 5). Average densities of chaetognaths and jellyfish during onshore winds are below the ctenophore densities tested (Fig. 7). Strong evidence of predator satiation was obtained (Fig. 6). The equation to predict larval mortality (y, %/d) is:

$$(1)\quad y = 26.51 - 3.3409 \ln (\text{no. of capelin larvae/m}^3),$$

$$R^2 = 0.51,\ P < 0.01,\ n = 9.$$

This effect, coupled with the reduction in predator densities in the water mass occupied by capelin (Fig. 5), should significantly reduce mortality due to predation during early larval drift in capelin.

Growth Responses

The effect of water mass replacement on the biomass of the edible zooplankton size fraction is depicted in Fig. 7 which portrays a simulation of the average biomass of this fraction at various growing degree days (calculated from April 1) and wind combinations. This simulation is based on the multiple regression model detailed in Table 2. The significant influence of wind condition at any stage in the growing degree day cycle is apparent.

To assess the potential effect of this elevation in edible zooplankton biomass on larval growth rates we again performed a series of enclosure experiments in which the biomass of edible zooplankton was manipulated. All enclosures were identical in design to those previously described. Twelve trials were performed in 1980. Four enclosures were constructed of <5 µm mesh. These were filled with 10 µm filtered seawater to produce below ambient edible zooplankton biomasses. The remaining eight enclosures were constructed of 150 µm nitex. All eight were allowed to fill with water which passed through the mesh. The zooplankton

biomass of six of these enclosures was enhanced by adding zooplankton collected with a ½-m, 150-μm standard plankton net towed at a velocity of <0.5 m·s^{-1}. Two enclosures received the contents of paired 18-m^3 samples, two the contents of paired 54-m^3 samples, and two the contents of paired 120-m^3 samples. All samples were passed through a 355-μm filter before addition. Zooplankton >355 μm was discarded. Six hundred and fifty yolk sac larvae were collected from the beach sediments for stocking in each enclosure. Six hundred were stocked and the remaining 50 were measured to the nearest 0.1-mm TL to determine the mean length at stocking in each enclosure. No significant difference in the mean length of stocked fish in the 12 enclosures was observed ($P > 0.05$). Duration of the trials was 7 d. The average water temperature was 6.5°C during these experiments. At the end of the trial the enclosures were lifted, the contents collected from the cod end, and the final size of the remaining larvae and the dry weight biomass of the <250-μm, 250- to 355-μm, and >355-μm size fractions were determined. Daily larval growth rate was correlated with the final biomass of the three zooplankton size fractions. Daily growth rates were strongly positively correlated with the biomass of the <250-μm size fraction ($r = 0.79$, $n = 12$, $P < 0.01$). No correlation was observed between larval growth rates and the biomass of the 250- to 355-μm ($r = -0.11$, $P > 0.05$) and >355-μm ($r = -0.46$, $P > 0.05$) size fractions, supporting our earlier assumptions regarding the importance of the <250-μm size fraction as food for larval capelin. The relationship between daily growth rates (y, mm/d) and the biomass of the <250-μm size fraction (x, μg/m^3) is illustrated in Fig. 8. The equation to predict larval growth rate is:

$$(2) \quad y = 0.0337 \ln X - 0.2524, \quad R^2 = 0.62, P < 0.01.$$

The potential effects of changes in food level resulting from water mass replacement were assessed by substitution of predictions of the average biomass of the edible zooplankton size fraction at varying times (growing degree days), and under varying wind conditions, into the model describing the relationship between food levels and daily growth rate (Fig. 8). The results, depicted in Fig. 9, indicate daily growth rates could be increased by up to eightfold under conditions of continuous onshore wind. A more realistic increase, given the nature of the wind patterns in eastern Newfoundland, is 1.2- to 5.5-fold. The effect of this increase in daily growth rate on larval survival is presently unquantified but is under investigation. Several authors have hypothesized that accelerated growth rates yield better survival because the larvae more rapidly pass through the size range at which they are most vulnerable to the suite of predators to which they are exposed (Ware 1975; Jones 1973).

At a more general level, it is worthy of note that the abundance of eggs and larvae of 11 marine fish species (*Tautogolabrus adspersus*, *Glyptocephalus cynoglossus*, *Gadus morhua*, *Hippoglossoides platessoides*, *Liparus atlanticus*, *Pseudopleuronectes americanus*, *Sebastes marinus*, *Clupea h. harengus*, *Myoxocephalus aenaeus*, *Ulvaria subbifurcata*, and *Stichatus punctatus*) represented in our plankton collections also showed a strong association with surface water masses (Fig. 3). Association with this water mass presumably conveys to them advantages similar to those experienced by capelin.

In our review of the literature on larval fish ecology we have been struck by the paucity of studies documenting reproductive and behavioral patterns which may minimize predator impact and maximize food availablility. Exceptions are the works by Bams (1969), Ware (1977), and Fortier and Leggett (1982). Such strategies, commonly exhibited among other organisms (Lloyd and Dybas 1966; Janzen 1969, 1971; Smith 1970; Giesel 1976), are probably more common among fishes than is currently evident. The lack of such examples among fishes stems, in part, from the survey approach to larval fish studies which are often of limited scope and typified by large-scale (spatial and temporal) sampling programs. Given these facts greater caution should be exercised when attempting to infer mechanisms from the results of such studies in the absence of a thorough understanding of the system dynamics; the inference that an inverse relationship between predator and larval fish abundances results from predation (Alvariño 1981; Möller 1980), or that a sudden change in larval densities in response to abrupt temperature or salinity changes, indicative of water mass exchange, is due to the temperature or salinity effect (Dickson et al. 1974: Postuma and Zijlstra 1974) being cases in point. Or, as Richard Barber, Duke University, has expressed it "physical and biological processes are in sequence, so understanding the ecosystem requires understanding the sequence. A [marine] biologist ... with no understanding of the meteorology or currents is just whistling in the dark" (Hartline 1980). We concur that the measurement scale must be reduced (in space and time), and that an ecosystem approach must be adopted if future studies are to be successful in defining the important physical and biological processes regulating the dynamics of larval fish populations.

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Les métaux lourds comme indicateurs d'origine géographique de l'anguille d'Amérique (*Anguilla rostrata*)

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MOREAU, G., ET C. BARBEAU. 1982. Les métaux lourds comme indicateurs d'origine géographique de l'anguille d'Amérique (*Anguilla rostrata*). Can. J. Fish. Aquat. Sci. 39: 1004–1011.

Des anguilles d'Amérique (*Anguilla rostrata*) ont été prélevées dans le fleuve Saint-Laurent et plusieurs de ses affluents. Les concentrations en métaux lourds (Cd, Co, Cr, Cu, Hg, Mn, Ni, Pb, Zn) dans les muscles ont été analysées en relation avec le site de collecte, l'âge, la taille et le poids des spécimens. Parmi les métaux lourds essentiels, le zinc, le cuivre et surtout le manganèse permettent de distinguer des échantillons selon leur origine. Dans le Saguenay, rivière contaminée par des rejets de mercure, il est possible de distinguer deux lots d'anguilles d'après leur teneur en mercure, leur taille et leur poids, ce qui laisse supposer que ces deux lots ont vécu dans des parties différentes du bassin hydrographique. Les concentrations en métaux dans les anguilles paraissent dépendre de la disponibilité de ces métaux dans les sédiments de fond. L'analyse par groupement flexible et coordonnées principales donne des groupes insuffisamment homogènes et distincts pour conclure à un patron spécifique des teneurs en métaux lourds pour toutes les origines différentes.

Mots clés: anguilles d'Amérique, métaux lourds, fleuve Saint-Laurent

MOREAU, G., ET C. BARBEAU. 1982. Les métaux lourds comme indicateurs d'origine géographique de l'anguille d'Amérique (*Anguilla rostrata*). Can. J. Fish. Aquat. Sci. 39: 1004–1011.

American eels (*Anguilla rostrata*) were sampled from the St. Lawrence River and many of its tributaries. Heavy metal concentrations (Cd, Co, Cr, Cu, Hg, Mn, Ni, Pb, Zn) in muscles were analyzed in relation to collection site, age, length, and weight of the specimens. Among the essential heavy metals, zinc, copper, and especially manganese can be used to distinguish the samples by their origin. In the Saguenay River, which is contaminated by mercury wastes, it is possible to distinguish two types of eels according to their mercury content, weight, and length leading to the hypothesis that these two types lived in different parts of the drainage system. The metal concentrations in the eels seem to depend on the availability of these metals in the bottom sediments. Analysis by flexible grouping and principal coordinates yields groups that are not sufficiently homogeneous and distinct to conclude to a specific pattern of heavy metal contents for all the different origins.

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L'IDENTIFICATION de différents stocks dans une population de poissons peut être faite par des méthodes variées dont une revue est faite par Ihssen et coll. (1981). Ces diverses méthodes peuvent être regroupées en deux catégories. L'une de celles-ci est fondée sur la reconnaissance des différentes expressions d'un polymorphisme méristique ou morphométrique, physiologique, éthologique, biochimique ou génétique. L'autre repose sur l'identification d'un marquage expérimental ou naturel. Dans ce dernier cas le marquage peut être assuré par des parasites ou par une empreinte chimique, Calaprice et coll. (1971), qui reflète les caractéristiques de l'environnement de chaque stock. Cette empreinte peut être identifiée sur les écailles (Klokov et Frolenko 1970; Bagenal et coll. 1973; Moreau et Barbeau 1979; Lapi et Mulligan 1981) ou sur des tissus non calcifiés (Fisheries Agency of Japan 1967; Calaprice 1971).

L'empreinte chimique dans les tissus reflète les caractéristiques naturelles des eaux, comme dans le cas des études précédentes, mais elle pourrait aussi être influencée par les apports polluants. Comme le suggèrent Calaprice et coll. (1971), on pourrait utiliser cette approche mais la récente

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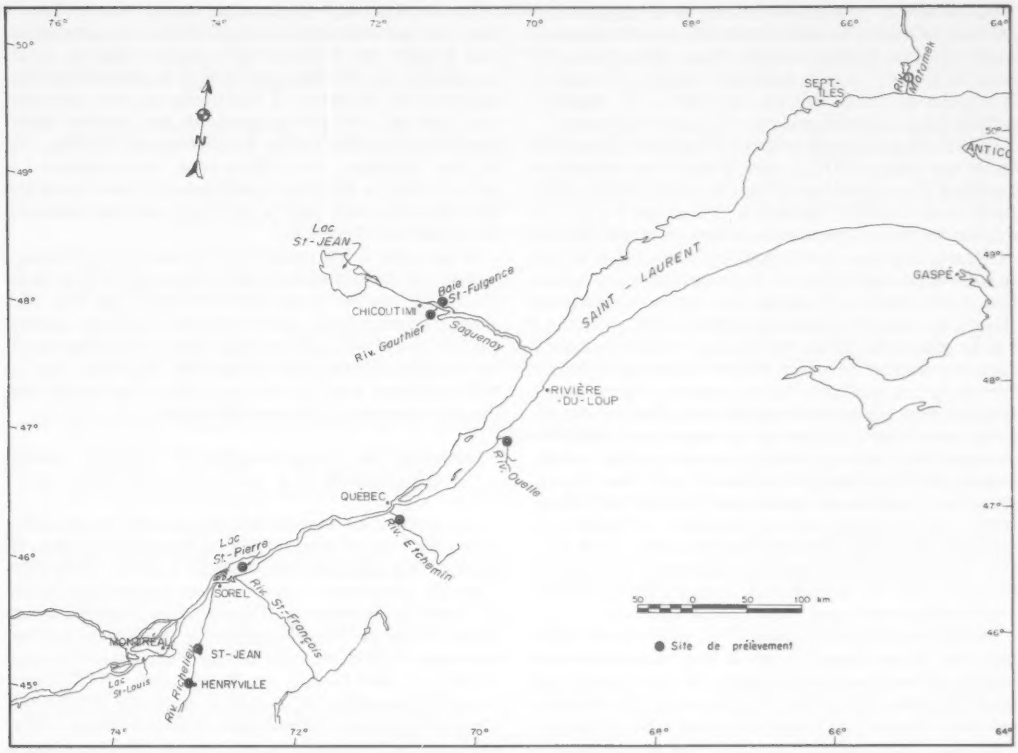

FIG. 1. Localisation des sites de prélèvements.

revue de Ihssen et coll. (1981) sur les méthodes d'identification des stocks ne mentionne aucun travail dans ce sens. Parmi les divers éléments polluants pouvant contribuer à un marquage le cas des métaux lourds paraît particulièrement intéressant. En effet les poissons ont la capacité de concentrer très fortement ces éléments, 6 à 7 000 fois selon Hannerz (1968), et cette concentration peut être affectée par les caractéristiques chimiques de l'eau, notamment la dureté (Wiener et Giesy 1979). D'autre part, l'analyse fréquente et routinière des métaux lourds lors du contrôle de qualité des espèces commerciales pourrait permettre de différencier les stocks. Il paraît donc intéressant de vérifier si la combinaison des concentrations de différents métaux rencontrés dans la chair des poissons peut fournir une empreinte permettant d'identifier divers stocks.

Pour vérifier cette hypothèse le cas des anguilles du bassin du Saint-Laurent paraît très approprié. La longue durée de vie, en rivière (12 ans en moyenne; Moreau, données personnelles non publiées), constitue un facteur favorable à l'établissement d'une empreinte chimique.

L'amplitude du bassin du Saint-Laurent et la diversité de la nature des bassins versants des affluents assurent la diversité des caractéristiques chimiques naturelles des eaux et des apports polluants ce qui devrait éventuellement permettre un marquage différent pour chaque stock.

Matériel et méthodes

Les prélèvements ont été réalisés dans cinq affluents du Saint-Laurent : les rivières Richelieu et Saint-François dans la portion fluviale, les rivières Ouelle et Saguenay dans l'estuaire moyen et la rivière Matamek dans le golfe, ainsi que dans le fleuve Saint-Laurent au niveau du lac Saint-Pierre et au niveau de la rivière Etchemin à Saint-Romuald (fig. 1). La nature des bassins de ces différentes rivières peut être caractérisée ainsi : agricole pour la rivière Richelieu, industriel et urbain pour la rivière Saint-François, industriel et forestier pour la rivière Saguenay, agricole et forestier pour la rivière Ouelle et forestier dans le cas de la Matamek.

Les spécimens de la Richelieu, considérés sédentaires, proviennent de pêches expérimentales réalisées à la hauteur de Henryville avant la période de migration soit durant les mois de mai et juin. Les spécimens de la Richelieu, considérés migrateurs, proviennent d'une pêche commerciale à Saint-Jean, pratiquée en juillet et en août, au moment de la migration reproductrice. Pour le Saguenay, un lot provient de la Baie de Saint-Fulgence et un autre de l'embouchure d'un petit affluent : la rivière Gauthier.

En plus des pêches commerciales les captures ont été réalisées par divers moyens : ligne de fond, nasse et verveuse, pêche électrique.

Au moment du prélèvement une tranche du corps est coupée avec un couteau en acier inoxydable, immédiatement en arrière de l'anus, et débarrassée de sa peau; elle est conservée congelée à −28°C jusqu'au moment de l'analyse. Le poids et la longueur de chaque individu sont notés et les otholithes prélevés pour la détermination de l'âge après calcination.

La mise en solution des métaux est faite selon la méthode décrite par Adrian (1973) à partir d'une coupe transversale d'environ 25 g placée dans 25 mL de HNO_3:$HClO_4$ (2:1). Après avoir chauffé le mélange à 55°C durant 4 à 5 h, on solidifie les graisses par immersion dans un bain de glace et on décante la solution. L'efficacité de l'attaque et de la mise en solution est supérieure à 90 %. Le dosage du mercure est fait sur un volume de 10 mL de cette solution à laquelle on ajoute 2 mL de H_2SO_4 et qui est chauffée à 50°C pendant 4 à 5 h. Le reste de la solution est maintenu à ébullition durant 2 à 3 h pour éliminer les vapeurs d'acide. Le dosage du manganèse et du zinc s'effectue sur des aliquotes diluées par un facteur 5 alors que les autres métaux sont dosés sur des aliquotes non diluées. Le mercure est analysé par absorption atomique sans flamme, à froid, et les autres métaux par absorption atomique dans une flamme air−acétylène. Un correcteur au deutérium est utilisé pour l'analyse des métaux cobalt, nickel, chrome, cadmium et plomb. La fidélité de la méthode a été vérifiée sur des échantillons de 5, 10 et 15 g, avec des coefficients de variation inférieurs à 5 % pour le dosage du zinc et du manganèse. L'absence d'effet de matrice a été confirmée par l'utilisation d'ajouts dosés.

Pour la comparaison des teneurs d'un métal entre les différents lots de spécimens, le test de Duncan (comparaisons multiples de moyennes) a été employé en choisissant le seuil de signification à $P > 0{,}01$. Le groupement des différents spécimens d'après leur teneur en métaux a été fait à partir d'une matrice de similarité calculée à l'aide du coefficient de Gower et le groupement flexible avec $\beta = -0{,}25$[1] a donné les meilleurs résultats par rapport aux essais de groupement à liens complets ou à liens intermédiaires. Enfin, une analyse en coordonnées principales a permis de situer les objets dans un espace réduit pour visualiser les relations de distance existant entre eux. Le choix de ces techniques est fait d'après Legendre et Legendre (1979).

Résultats et discussion

Relation entre la teneur en métaux et l'âge, le poids ou la taille

Il existe des différences significatives d'âge, de poids et de taille entre certains échantillons (tableau 1). Afin de vérifier si ces différences pouvaient influencer les variations de teneurs en métaux, des corrélations entre l'âge, le poids ou la taille des poissons et la teneur en différents métaux ont été calculées. Les valeurs des différents coefficients de corrélation (tableau 2) indiquent que les corrélations sont très rarement significatives avec l'âge mais le sont généralement, et de façon négative, avec le poids ou la taille. De telles corrélations ont été observées (Wiener et Giesy 1979; Bohn et McElroy 1976) pour diverses autres espèces lorsque l'on se réfère au corps entier et non uniquement au muscle. Toutefois, bien que statistiquement significatives, les corrélations sont toujours très faibles et les variables taille ou poids n'expliquent au maximum que 14 % de la variance dans les concentrations en métaux. L'interférence de cette variabilité avec celle due à l'origine géographique doit donc être faible et peut être considérée comme non déterminante. En effet, s'il en était autrement, les différences de concentrations en métaux entre les différents échantillons devraient suivre les différences existantes pour la taille ou le poids des individus de ces mêmes échantillons.

D'autre part, il faut souligner que le manganèse et le mercure ne sont pas significativement corrélés avec la taille ou le poids mais seulement et très faiblement avec l'âge. Une telle absence de corrélations pour le mercure a déjà été signalée par Establier (1975), qui mentionne que la concentration en mercure dans les anguilles européennes augmente avec la taille seulement pour les petits individus et qu'ensuite elle demeure constante ou régresse légèrement.

Variabilité des concentrations en métaux lourds selon l'origine

La concentration moyenne pour chaque métal est très différente selon l'origine géographique des échantillons (tableau 1) comme l'ont déjà mentionné Romeril et Davis (1976) pour l'anguille européenne. Ces différences peuvent être reliées au degré de pollution de l'eau puisque l'absorption des métaux lourds par l'anguille semble de faire surtout par voie branchiale à partir de l'eau comme l'ont montré Hannerz (1968) et Noël-Lambot et Bouquegneau (1977) chez l'anguille européenne et Keckes et Miettinen (1972) chez l'anguille japonaise. D'autre part, Wiener et Giesy (1979) ont conclu que la concentration des métaux chez les poissons dépendait d'autres facteurs que le régime alimentaire ou le niveau trophique.

Les sédiments peuvent aussi contribuer à la concentration des métaux dans l'eau, du moins pour le mercure, puisque Gillespie et Scott (1971) et Bisogni et Lawrence (1975) ont montré que les formes inorganiques pouvaient être transformées en formes solubles sous l'action bactérienne en condition aérobique ou anaérobique. Le cadmium, le chrome et le cobalt, toujours présents en très faibles concentrations, voisines du seuil de détection des méthodes analytiques, présentent peu de différences entre lots et sont donc de ce fait peu discriminants dans notre étude.

Le cuivre, le nickel et le plomb sont aussi généralement peu abondants mais permettent toutefois de discriminer différents groupes d'échantillons.

Les teneurs élevées en cuivre des anguilles de la rivière Saint-François peuvent être reliées à l'exploitation d'une mine dans la partie amont. Les suspensoïdes de cette rivière contiennent jusqu'à 500 μg/g de cuivre (Bisson et al. 1979) dont plus de la moitié est liée à la matière organique.

Le nickel se trouve en faible concentration dans les anguilles de la rivière Saint-François, bien que les suspensoïdes de cette rivière contiennent autant de nickel que de cuivre (Bisson et al. 1979). Cependant, la fraction du nickel liée à la matière organique est inférieure à 5 %, et moins de 10 % du nickel et du cuivre est lié aux fractions dites échangeables et carbonatées. Il est intéressant de noter que les anguilles du

[1]Voir Legendre et Legendre (1979) pour le détail de la formule et la signification de ce coefficient.

TABLEAU 1. Comparaison des âges, taille, poids et concentrations en différents métaux entre les différents lots.[a]

Âge, ans	S.F. (15) 9,8 (2,18)	M. (13) 12,1 (2,93)	R.O. (4) 12,5 (2,64)	S.G. (19) 13,4 (2,95)	S.P. (7) 13,6 (2,37)	S.R. (13) 14,1 (2,72)	R.s. (61) 14,6 (2,75)	R.m. (36) 15,3 (3,82)	S.Fu. (16) 15,4 (2,36)
Taille, cm	M. (13) 449,5 (92,52)	S.G. (19) 565,0 (97,78)	S.Fu. (16) 694,1 (97,90)	R.O. (4) 717,7 (43,15)	S.F. (15) 725,9 (49,97)	R.s. (61) 754,8 (62,02)	R.m. (36) 780,9 (73,67)	S.P. (7) 897,6 (79,81)	S.R. (13) 897,9 (75,51)
Poids, g	M. (13) 174,5 (100,0)	S.G. (19) 334,2 (174,4)	S.Fu. (16) 694,1 (138,1)	R.O. (4) 731,2 (188,6)	S.F. (15) 873,3 (169,1)	R.s. (61) 898,8 (264,2)	R.m. (36) 1003,0 (282,9)	S.P. (7) 1696,4 (499,2)	S.R. (13) 1703,8 (518,5)
Cd, µg/g	S.R. (13) 0,005 (0,000)	S.F. (15) 0,006 (0,002)	R.s. (61) 0,006 (0,002)	S.P. (7) 0,007 (0,006)	R.m. (36) 0,022 (0,017)	R.O. (4) 0,029 (0,016)	S.Fu. (16) 0,033 (0,029)	S.G. (19) 0,033 (0,029)	M. (13) 0,039 (0,042)
Cr, µg/g	S.P. (7) 0,005 (0,000)	R.s. (61) 0,005 (0,001)	S.R. (13) 0,008 (0,006)	S.G. (19) 0,017 (0,022)	R.m. (36) 0,017 (0,019)	S.F. (15) 0,020 (0,013)	S.Fu. (16) 0,021 (0,022)	R.O. (4) 0,029 (0,026)	M. (13) 0,032 (0,017)
Co, µg/g	S.P. (7) 0,009 (0,005)	R.s. (61) 0,011 (0,007)	S.R. (13) 0,015 (0,010)	S.F. (15) 0,016 (0,010)	R.O. (4) 0,030 (0,041)	R.m. (36) 0,035 (0,029)	S.G. (19) 0,048 (0,038)	S.Fu. (16) 0,059 (0,035)	M. (13) 0,059 (0,043)
Cu, µg/g	R.s. (61) 0,436 (0,149)	R.m. (36) 0,450 (0,113)	R.O. (4) 0,450 (0,154)	S.R. (13) 0,500 (0,129)	S.G. (19) 0,516 (0,112)	S.Fu. (16) 0,537 (0,154)	S.P. (7) 0,614 (0,107)	M. (13) 0,646 (0,250)	S.F. (15) 0,720 (0,278)
Pb, µg/g	S.P. (7) 0,050 (0,000)	S.R. (13) 0,054 (0,053)	R.O. (4) 0,125 (0,050)	S.F. (15) 0,147 (0,114)	S.G. (19) 0,178 (0,119)	R.m. (36) 0,181 (0,113)	R.s. (61) 0,241 (0,216)	M. (13) 0,314 (0,218)	S.Fu. (16) 0,344 (0,126)
Ni, µg/g	S.F. (15) 0,220 (0,192)	R.s. (61) 0,300 (0,291)	S.R. (13) 0,492 (0,233)	S.P. (7) 0,643 (0,151)	R.m. (36) 0,736 (0,199)	S.G. (19) 0,795 (0,253)	R.O. (4) 0,925 (0,330)	M. (13) 1,000 (0,458)	S.Fu. (16) 1,394 (0,807)
Mn, µg/g	S.G. (19) 0,347 (0,107)	S.P. (7) 0,557 (0,315)	S.Fu. (16) 0,894 (0,370)	M. (3) 1,015 (0,708)	R.m. (36) 1,075 (0,972)	S.R. (13) 1,108 (0,696)	R.O. (4) 1,225 (0,596)	R.S. (61) 1,410 (0,699)	S.F. (15) 2,573 (1,369)
Hg, µg/g	S.F. (15) 0,131 (0,131)	R.s. (61) 0,310 (0,263)	R.m. (36) 0,319 (0,213)	M. (13) 0,331 (0,103)	R.O. (4) 0,475 (0,050)	S.R. (13) 0,501 (0,147)	S.P. (7) 0,776 (0,299)	S.G. (19) 1,253 (0,978)	S.Fu. (16) 1,994 (0,869)
Zn, µg/g	R.O. (4) 23,0 (1,96)	M. (13) 24,2 (1,15)	S.G. (19) 29,8 (1,98)	R.m. (36) 30,5 (7,22)	R.s. (61) 31,7 (4,93)	S.Fu. (16) 33,8 (2,02)	S.R. (13) 35,2 (1,26)	S.F. (15) 39,6 (1,94)	S.P. (7) 41,3 (2,81)

[a]Les lots soulignés ne présentent pas de différences significatives entre eux au seuil de 0,01. Les chiffres entre parenthèses à côté de l'origine géographique représentent le nombre d'individus. La moyenne en µg/g de poids frais et l'écart type (entre parenthèses) sont indiqués en dessous de la désignation d'origine. R.s. = Richelieu, sédentaires; R.m. = Richelieu, migratrices; R.O. = Rivière Ouelle; S.G. = Rivière Saguenay à l'embouchure de la rivière Gauthier; S.Fu. = Rivière Saguenay dans la baie de St-Fulgence; M = Rivière Matamek; S.F. = Rivière St-François; S.R. = Fleuve St-Laurent à St-Romuald; S.P. = Fleuve St-Laurent dans le lac St-Pierre.

TABLEAU 2. Corrélation entre taille, poids ou âge et les différents métaux pour l'ensemble des spécimens (n = 184).(ns = non significatif; * = $P < 0,05$; ** = $P < 0,01$.

	Cr	Co	Ni	Cu	Zn	Cd	Hg	Pb	Mn
Taille	−0,203**	−0,378**	−0,296**	−0,195**	0,351**	−0,376**	ns	−0,292**	ns
Poids	−0,171**	−0,323**	−0,241**	ns	0,308**	−0,342**	ns	−0,319**	ns
Âge	ns	ns	ns	−0,271**	ns	ns	0,179*	ns	−0,270**

Saguenay à Saint-Fulgence sont les plus contaminées en nickel.

Le plomb se retrouve en faible quantité dans les anguilles de la rivière Saint-François en dépit de la présence de rejets miniers contenant du plomb dans la partie amont de la rivière mais il faut mentionner que Bisson et al. (1979) ont observé que moins de 20% du plomb des suspensoïdes de cette rivière est lié à des phases solubles. Les anguilles des rivières Richelieu, Matamek et Saguenay sont plus riches en plomb que celles de la rivière Saint-François. Puisque l'absorption du plomb par les poissons s'effectue surtout à partir de la forme ionique (Berg et al. 1973) et que le plomb est difficile-

ment libéré des sédiments (Lee et al. 1975) il apparaît difficile d'expliquer par les seuls apports locaux, les teneurs élevées de plomb dans les anguilles d'une rivière aussi exempte de pollution industrielle que la rivière Matamek. Cependant, le transport sur longue distance de polluants atmosphériques et leurs retombées dans les zones nordiques, comme il a été mis en évidence pour le plomb, dans les sédiments de la rivière et du lac Matamek (Ouellet et Poulin 1977) et dans les sédiments du Saguenay (Barbeau et al. 1981b) expliqueraient, non seulement les teneurs plus élevées en plomb dans les anguilles des rivières Matamek et Saguenay, mais aussi la tendance à des concentrations plus élevées en nickel et en cuivre.

Le manganèse dans les individus de la rivière Saint-François est très élevé, à l'opposé des concentrations observées chez les anguilles du Saguenay. Contrairement au plomb, le manganèse des sédiments peut assez facilement passer en solution (Lee et al. 1975). Dans la rivière Saint-François, plus de la moitié du manganèse dans les suspensoïdes se trouve dans la fraction soluble en milieu acétique (Bisson et al. 1979). Nous avons effectué des extractions à l'acide acétique sur 10 échantillons de sédiments de fond de la rivière Saint-François. Ces essais ont libéré 40 μg/g de manganèse alors que la concentration dans les anguilles de cette rivière se situe à 2,6 μg/g. Des essais similaires effectués sur des sédiments du Saguenay, à l'embouchure de la rivière Gauthier, ont libéré 13 μg/g de manganèse en regard d'une concentration moyenne de 0,35 μg/g dans les anguilles. Ces résultats tendent à indiquer que la biodisponibilité d'un métal est reliée à la solubilisation de celui-ci à partir des sédiments.

Les teneurs en mercure sont assez faibles et inférieures à la limite permise pour la consommation (0,5 μg/g) pour la majorité des prélèvements; seuls les individus provenant du lac Saint-Pierre et du Saguenay dépassent les normes admises et les individus provenant du Saguenay (rivière Gauthier ou Saint-Fulgence) sont remarquables par de très fortes concentrations (en moyenne 1,3 et 2,0 μg/g respectivement). Les valeurs enregistrées pour les individus prélevés à Saint-Fulgence sont très significativement différentes de toutes les autres, et celles correspondant aux anguilles de la rivière Gauthier sont également distinctes de toutes les autres au seuil de 0,05.

Les teneurs élevées en mercure des individus du lac Saint-Pierre peuvent être mises en relation avec la contamination mercurielle importante des eaux et des sédiments du Saint-Laurent au niveau du lac Saint-Louis (Carignan et Alves 1978) et du lac Saint-Pierre (CENTREAU 1974). Il en est de même pour les individus du Saguenay où 13 des 16 spécimens de la Baie de Saint-Fulgence et 10 des 19 de l'embouchure de la rivière Gauthier contiennent plus de 0,9 μg/g de mercure. Dans cette région, les déversements de mercure ont été importants jusqu'en 1970 et ont contaminé les sédiments (Loring 1975), mais depuis 1971, on observe une baisse continuelle de la concentration en mercure dans les sédiments tout le long du Saguenay (Barbeau et al. 1981b) à la suite de la suppression des apports et grâce aux forts taux d'accumulation des suspensoïdes dans les zones préalablement contaminées (Smith et Walton 1980; Barbeau et al. 1981a). On peut donc prévoir, qu'avec le temps, la concentration de mercure dans les poissons du Saguenay devrait diminuer suivant la même évolution que celle observée dans le lac Érié (Ontario

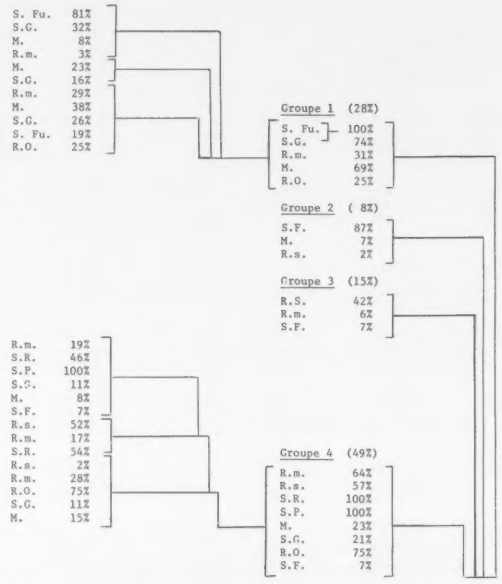

FIG. 2. Représentation schématique du groupement flexible. L'importance des groupes 1, 2, 3, 4 par rapport à l'ensemble des échantillons est indiquée, en pourcentage, à côté de son identification. Les pourcentages associés à chaque origine géographique indiquent la proportion d'individus de cette origine qui sont compris dans le groupe ou le sous-groupe. Les groupes 2 et 3 étant très homogènes, les sous-groupes n'ont pas été représentés. La notation de l'origine géographique est identique à celle du tableau 1.

Ministry of Environment 1977) où la contamination des sédiments diminue depuis 1970 (Thomas et Jaquet 1976).

En raison de l'âge élevé des anguilles (15 ans), et de la difficulté qu'ont les poissons d'éliminer le mercure (Sharpe et al. 1977), les teneurs de mercure supérieures à 0,9 μg/g s'expliquent aisément chez les spécimens vivant au contact des sédiments du Saguenay. Il paraît surprenant, cependant, de constater qu'environ la moitié des anguilles pêchées à l'embouchure de la rivière Gauthier contiennent moins de 0,5 μg/g de mercure, d'autant plus que l'âge moyen de ces spécimens est élevé et que les teneurs des autres métaux ne sont pas statistiquement différentes ($P > 0,05$) de l'ensemble des autres échantillons. La petite taille des anguilles ne peut expliquer les faibles teneurs en mercure puisque Establier (1975), de Freitas et Hart (1977) ont montré que l'accumulation de mercure était plus rapide chez les poissons de petite taille. Il semble donc que les anguilles de petite taille et pauvres en mercure, pêchées dans le Saguenay, ont séjourné la majeure partie de leur existence dans des tributaires ou dans des sections de la rivière exempts de pollution mercurielle et qu'elles étaient en migration lors de leur capture à l'embouchure de la rivière Gauthier.

Le zinc se trouve en concentration élevée dans tous les groupes d'anguilles, mais on observe une tendance aux plus fortes teneurs dans les anguilles de cours d'eau où les rejets industriels et urbains sont les plus élevés. Cette relation entre

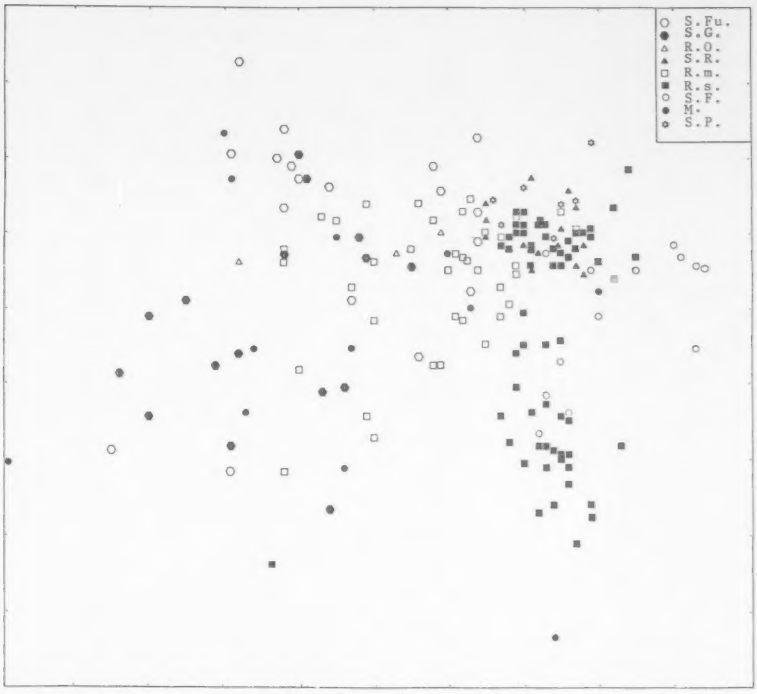

FIG. 3. Représentation schématique de la distribution des spécimens selon l'analyse en coordonnées principales. La notation de l'origine géographique est identique à celle du tableau 1.

milieux pollués et teneurs élevées en zinc a déjà été observée dans les poissons de la région de Toronto (Brown et Chow 1977) et dans les poissons de lacs voisins de rejets miniers (Falk et coll. 1973). Les variations temporelles et spatiales de zinc dissous étant élevées (Etcheber 1978), il est difficile d'utiliser le zinc pour des fins de discrimination.

Il semble que la théorie de la régulation homéostatique des métaux essentiels, proposée par Cross et coll. (1973) et par Wiener et Giesy (1979), ne s'applique pas aux concentrations observées ici pour les métaux cuivre, manganèse et zinc.

De façon qualitative, il ressort du tableau 1 que quelques métaux sont plus concentrés chez certaines anguilles et que dans certains cas il est possible d'utiliser un élément métallique comme indicateur géographique, comme par exemple le manganèse pour la rivière Saint-François et le mercure pour le Saguenay.

VARIABILITÉ DE L'ENSEMBLE DES MÉTAUX SELON L'ORIGINE

Il semble intéressant de compléter cette analyse en déterminant si la combinaison de concentrations en différents métaux permet de définir un patron global qui soit caractéristique d'une origine géographique donnée. Pour vérifier une telle éventualité, nous avons regroupé les différents individus à partir de leur similarité de concentrations en métaux.

Le groupement flexible permet de définir quatre grands groupes présentant un faible lien entre eux mais à l'intérieur desquels les similarités de fusion sont fortes (fig. 2).

Si les individus d'une même origine géographique étaient caractérisés par un patron net de teneurs en métaux, on devrait retrouver autant de groupes que de lots d'origine géographique différente ou du moins tous les individus provenant d'une même rivière devraient se retrouver dans le même groupe. La réalité est plus nuancée comme l'indique la figure 2.

Les individus du Saguenay sont rassemblés à 86 % dans le groupe 1 à l'intérieur duquel on peut distinguer 2 sous-groupes, l'un renfermant 87 % des individus en provenance de la Baie de Saint-Fulgence et l'autre 42 % de ceux provenant de l'embouchure de la rivière Gauthier. Ce fort taux de regroupement des spécimens du Saguenay indique donc que dans cette rivière les anguilles possèdent une combinaison de concentrations en métaux lourds bien caractéristique qui les distingue des autres échantillons. Les 14 % non classifiés dans le groupe 1 se retrouvent dans le groupe 4 et proviennent tous du lot prélevé dans l'embouchure de la rivière Gauthier; il est donc possible que ces individus aient passé la majorité de leur vie dans cette rivière, ce qui expliquerait le patron différent de celui du Saguenay. Cette hypothèse de l'origine géographique différente des spécimens est appuyée par la grande variabilité inter-individuelle des concentrations en mercure de ces animaux.

Les poissons de la Saint-François se retrouvent à 87 % dans le groupe 2 qui est presque exclusivement constitué de ces

individus. Les 13 % restant se répartissent entre les groupes 3 et 4.

Les individus identifiés comme sédentaires (prélevés en mai–juin par la pêche expérimentale) dans le Richelieu se répartissent entre les groupes 3 (42 %) et un des sous-groupes du groupe 4 (53 %) alors que ceux identifiés comme migrateurs (prélevés en juillet–août dans la pêche commerciale) se répartissent entre les groupes 1 (30 %) et 4 (69 %). L'appartenance des migrateurs à deux groupes très distincts s'explique bien puisqu'ils peuvent provenir d'origines différentes à l'intérieur du bassin de la Richelieu et du lac Champlain. (Il faut mentionner que le lac Champlain est en communication avec la rivière Richelieu (affluent du Saint-Laurent) et la rivière Hudson qui se jette dans l'Atlantique et qu'il existe des populations migratrices dans les deux rivières). En revanche, la répartition des sédentaires en deux groupes est plus difficilement explicable; toutefois il faut remarquer que les groupes 2 et 4 sont beaucoup plus proches que les groupes 1 et 4 qui se partagent les migrateurs.

Les spécimens provenant du Saint-Laurent (prélèvement à Saint-Romuald et lac Saint-Pierre) se retrouvent à 100 % dans le groupe 4, ceux du lac Saint-Pierre étant groupés exclusivement dans le 1er sous-groupe du groupe 4. Le 4^{e} sous-groupe du groupe 4 renferme 73 % des individus de la rivière Ouelle. Une analyse en coordonnées principales (fig. 3) de la matrice de similarités basée sur les concentrations en métaux lourds permet de retrouver les différents groupes et indique clairement, que si certains groupes sont assez bien séparés, d'autres, se chevauchant, sont peu discernables.

Il est donc possible de dire que dans l'ensemble, le regroupement des individus provenant de la même rivière est assez bon, démontrant ainsi une homogénéité du patron de teneur en métaux. En revanche, des individus d'origines différentes peuvent être classifiés dans le même groupe démontrant une non spécificité de leur patron de métaux lourds.

L'emploi des métaux lourds comme indicateurs d'origine géographique paraît donc applicable pour identifier certaines rivières, telles que le Saguenay et la Saint-François dans le cas présent. Il est vraisemblable que les mêmes analyses appliquées à un ensemble d'anguilles dont les origines seraient plus différentes permettraient une meilleure discrimination.

Remerciements

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Energetics of Sablefish, *Anoplopoma fimbria*, under Laboratory Conditions

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SULLIVAN, K. M., AND K. L. SMITH JR. 1982. Energetics of sablefish, *Anoplopoma fimbria*, under laboratory conditions. Can. J. Fish. Aquat. Sci. 39: 1012–1020.

We measured respiration, growth, ingestion, and excretion rates for sablefish, *Anoplopoma fimbria*, collected off southern California at a depth of 500 m and maintained in the laboratory. We also measured the water, protein, and lipid content of white skeletal muscle in both laboratory-held and field fish. Sablefish fed a large ration (14% of wet body weight) every 7–10 d showed growth rates two to three times higher than known growth rates for field fish. On a reduced ration (4% of wet body weight) sablefish grew at rates similar to field fish, but white muscle composition varied significantly from field fish. Oxygen consumption rates under constant temperature conditions showed a decrease in the weight-specific oxygen consumption rates with increase in body weight, ranging from routine metabolic rates of 195.8 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ for a 0.25-kg fish to 60.8 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ for a 2.78-kg fish. Based on measurements of respiration and excretion, sablefish were estimated to have 162 d of energy stored in the body lipids and did not show signs of starvation stress with food deprivation up to 6 mo in the laboratory. Energy allocation shows very slow growth rates, low conversion efficiencies, and low metabolic rates as adjustments made to large, infrequent meals.

Key words: physiological responses, benthopelagic fish, growth, metabolic rate, respiration, excretion

SULLIVAN, K. M., AND K. L. SMITH JR. 1982. Energetics of sablefish, *Anoplopoma fimbria*, under laboratory conditions. Can. J. Fish. Aquat. Sci. 39: 1012–1020.

Nous avons mesuré les taux de respiration, de croissance, d'ingestion et d'excrétion chez des morues charbonnières, *Anoplopoma fimbria*, capturées au large de la Californie méridionale à une profondeur de 500 m et maintenues en laboratoire. Nous avons également déterminé la teneur en eau, en protéines et en lipides du muscle squelettique blanc chez des poissons maintenus en laboratoire ainsi que sur le terrain. Les morues charbonnières auxquelles on donne une nourriture abondante (14% du poids corporel humide) à tous les 7–10 jours croissent à un rythme de deux à trois fois plus rapide que dans la nature. Avec ration limitée (4% du poids corporel humide) la morue charbonnière croît à des taux semblables à ceux de poissons sur le terrain, mais la composition du muscle blanc est nettement différente de celle de ces derniers. Les taux de consommation d'oxygène spécifique au poids, à des températures constantes, diminuent à mesure qu'augmente le poids corporel, variant de taux métaboliques routiniers de 195,8 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ chez un poisson de 0,25 kg à 60,8 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ chez un poisson de 2,78 kg. En se fondant sur des mesures de respiration et d'excrétion, on estime à 162 jours l'énergie entreposée sous forme de lipides corporels. D'après ces mesures également, il n'y a pas de stress à la suite d'un jeûne en laboratoire pouvant durer jusqu'à 6 mois. Comme ajustements à des repas volumineux et peu fréquents, la morue charbonnière répartit son énergie entre des taux de croissance très lents, de faibles rendements de conversion alimentaire et de faibles taux métaboliques.

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LABORATORY studies can provide important types of information on fish energetics not generally obtainable from field studies. The range of growth, and metabolic and excretion rates measured under controlled laboratory conditions offer insights into the physiological scope of a marine fish which may have some predictive value as to the ecology of the fish in its own environment. Subsequently, energetics studies often serve to illustrate the biological adaptations utilized by a species to cope with one particular biotic or abiotic factor in the environment. Therefore, one way of understanding the physiological consequences of a limited food supply or large infrequent rations, for example, would be to investigate the energetics of a species under such conditions in the laboratory.

Energetics studies of sablefish, *Anoplopoma fimbria*, were

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TABLE 1. Proximate chemical composition of squid, Pacific mackerel, and synthetic foods used in *Anoplopoma fimbria* growth experiments. All values are expressed as percent wet weight with standard deviation and sample size. Joules per gram of food are calculated from average composition and conversion of 18.8×10^3 J·g^{-1} protein and $33.5 \text{ J} \times 10^3 \cdot \text{g}^{-1}$ lipid (Brett and Groves 1979).

Food	*n*	Water, %	Protein, %	Lipid, %	Energy, kJ·g^{-1}
Squid (*Loligo opelensus*)	12	82.0±3.3	11.4±2.7	2.3±1.6	2.92
Pacific mackerel (*Scomber japonicus*)	16	72.5±4.2	18.6±3.7	3.0±2.4	4.51
High lipid synthetic diet	23	76.0±2.1	4.8±2.2	16.0±1.9	6.26
No-calorie synthetic diet	17	96.0±1.4	1.2±0.7	0.0±0	0.23

initiated to learn more about the energy allocation of a relatively deep-living benthopelagic fish. Large deep-living benthopelagic fishes such as macrourids are known to feed on large episodic carcass falls and have extremely low metabolic rates, 2 orders of magnitude lower than comparable-sized shallow-living fish when attracted to baited in situ respirometry chambers (Smith 1978). Sablefish has an extremely broad geographic range along the continental slope from Mexico to the Bering Sea and westward to Japan. Its bathymetric distribution is equally broad, extending from the surface water in the northernmost areas of its range to over 1550 m off southern California (Hart 1973; Phleger et al. 1970). Sablefish belong to the family Anoplomatidae (Order Scopaeniformes) which has two monotypic genera. The skilfish (*Erilepis zonifer*), the other family member, is also a deep-living fish, but does not occur south of Monterey Bay, California; both species show greatest abundance off Alaska. Because it has no swim bladder, sablefish can be brought to the surface in good physiological condition unlike most deep-living fishes.

Field data have been collected on the food relationships and general population ecology of sablefish off southern California (Conway 1967) and off Oregon and Washington (Holmberg and Jones 1954; Pruter 1954). An attempt to hold sablefish in large floating pens off British Columbia succeeded in maintaining a large number of fish over a period of several years on a diet of Pacific herring (*Clupea harengus pallasi*) and chopped spiny dogfish (*Squalas acanthias*) (summarized by Kennedy 1974). However, sablefish has not been studied under laboratory conditions, especially with respect to its ability to thrive on large (15% of wet weight), infrequent meals. Measurements of growth, and metabolic or excretion rates have not been made on individual fish.

The purpose of this study was to examine the physiological responses of sablefish collected off southern California and maintained in the laboratory on varying ration levels fed at 7- to 10-d intervals. Along with the aquarium studies, we made corresponding biochemical analyses of muscle tissue composition. This study offers insights into the changes, both physiological and biochemical, that occur as a fish inhabits greater depths and experiences potentially lower rations and longer intervals between meals.

Materials and Methods

All *A. fimbria* used in the aquarium experiments were collected from Scripps Canyon off San Diego, California, at a depth of 468 m with the exception of one 0.25-kg fish caught in Monterey Bay, California. All fish were collected on either electric fishing reels or longlines, and transported back to the laboratory in chilled water. In the laboratory, fish were held in 2100-L chilled running seawater tanks which had seasonal temperature fluctuations ranging from 6.0 to 10.0°C. These tanks were located in a darkened enclosure and were covered to minimize disturbances. All fish, both experimental fish and field fish killed for biochemical assays were collected in June or November.

Within the tanks, sablefish were confined individually by nylon mesh barriers to minimize activity and to identify individuals. Typically, fish occupied a space $1.0 \times 0.5 \times 0.8$ m. Tanks were cleaned once a week; however, there was very little fouling over the 4- to 6-mo experiments because of the darkness and the chilled water. Fish were fed every 7–10 d; three separate experiments were conducted, each with four to eight fish.

Experiment I ran from November 1978 to June 1979 with four fish fed a ration of chopped mackerel and squid. Two fish were killed after 100 d, and the remaining two fish were killed after 209 d. The purpose of this experiment was to evaluate laboratory survival and maximum growth rates on weekly feedings.

Experiment II ran from June 1979 until December 1979 with six fish fed chopped mackerel every 8–10 d; two fish starved that entire period of time. The purpose of this experiment was to evaluate growth on varying ration size and time course of starvation.

Experiment III ran from November 1979 to April 1980 with seven fish fed synthetic diets (mackerel puree, corn oil and agar, and a filler food with just agar). The purpose of this experiment was to look at varying composition of ration and starvation; fish were fed every 8–10 d.

The composition of the various foods was assayed and is given in Table 1 along with energy content of food. After 24 h, any uneaten food was removed from the tanks, dried, and weighed. Controls were run with all food items where the loss of weight with soaking times of 6, 12, and 24 h was measured; there was no significant loss of weight in any of the food (Student's *t*-test $P = 0.05$). Mackerel used were eviscerated and sliced into 3-cm slices. Ingestion rates were determined by subtracting the uneaten food from total ration given to the fish.

TABLE 2. Growth, ingestion, and conversion efficiencies of laboratory *Anoplopoma fimbria* from three growth experiments. The diet in experiment I was chopped mackerel and squid, the diet in experiment II was chopped mackerel, and the diet in experiment III was synthetic high lipid food and synthetic filler food. Conversion efficiency is defined as kilograms wet body weight gained per kilogram food.

Initial weight, kg	Final weight, kg	Ration, (g/wk)	Ingestion (avg. g/wk eaten), $\bar{x}$ ±SD	Months observed	kg gained per month	Conversion efficiency
			Experiment I			
1.88	2.32	200	118.3±54	3.3	0.070	0.15
1.80	2.24	200	118.2±41	6.9	0.066	0.17
1.69	2.17	200	116.6±58	3.3	0.075	0.17
1.38	1.83	200	101.0±38	6.9	0.085	0.20
			Experiment II			
2.14	2.80	350	179.2±63	7.2	0.091	0.12
1.96	2.70	350	173.6±67	5.8	0.128	0.17
1.35	1.57	200	123.2±45	5.8	0.041	0.08
1.44	1.57	90	66.5±39	5.8	0.022	0.08
1.35	1.24	90	58.1±23	5.8	−0.019	—
1.57	1.45	0	0	5.8	-0.020	—
0.81	0.69	0	0	5.8	−0.021	—
			Experiment III — High lipid			
2.25	2.37	250	241.0±46	4.0	0.029	0.03
1.09	1.17	200	166.5±37	4.0	0.020	0.03
0.99	1.10	200	175.0±42	4.0	0.028	0.04
			Experiment III — Filler food			
1.91	1.79	200	178.4±44	4.0	−0.029	—
1.90	1.74	200	175.7±33	4.0	−0.040	—
1.80	1.68	200	184.3±37	4.0	−0.030	—

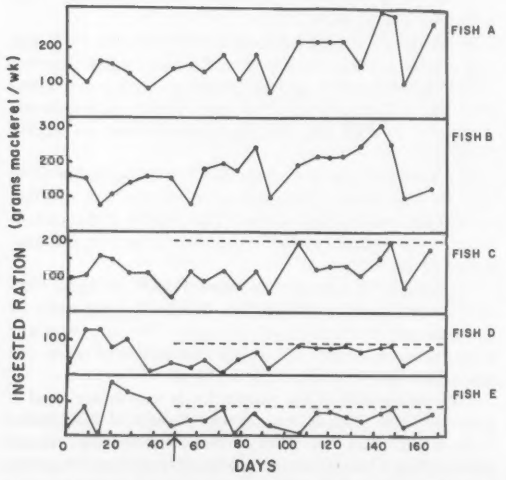

FIG. 1. Ingestion rates of *Anoplopoma fimbria* in Experiment II. Broken lines represent restricted ration levels; fish E received 80 g of chopped mackerel per week, fish D received 90 g/w, fish C received 200 g/w. Fish A and B were essentially on unlimited rations. Maximum ingestion rate for any 1-wk period was 330 g mackerel. Ration limitations were imposed after day 50 for fish C, D, and E.

GROWTH OF *ANOPLOPOMA FIMBRIA*

Growth of *A. fimbria* was monitored by weighing fish every 2−3 wk and by measuring changes in chemical composition of the white skeletal muscle. Fish were weighed in a handling net tared on a 9-kg-capacity scale calibrated in 10-g increments. The fish were not anesthetized before weighing, but were removed quickly with a wet handling net, weighed, and returned to the water in less than 4 min. The fish occasionally regurgitated food or refused to eat for periods up to 2 wk after this handling, but controls run on fish not weighed for 6 mo compared to fish weighed biweekly showed no significant differences in growth rates ($n = 3$, Student's t-test, $P = 0.05$) over a 6-mo period.

A second qualitative estimate of growth involved measuring changes in the gross chemical composition of white muscle after a fish had been on a specific dietary regime for the experimental period. When fish were collected from the field for a given experiment, five individuals were sacrificed immediately, and muscle tissue assayed as wild fish for comparison to experimental fish held in the laboratory.

Water contents were determined from two 1-g muscle samples taken from frozen tissue according to the procedure outlined in Sullivan and Somero (1980). Protein concentration of white muscle was determined using a modified micro-biuret method (Itzhati and Gill 1964) also described in Sullivan and Somero (1980). Lipid contents of white muscle was deter-

mined by a chloroform/methanol extraction and a simple charring method (Marsh and Weinstein 1966). Tripalmitin was used as a standard.

Respiration and Excretion

Oxygen consumption rates were determined by placing individual fish in a respiration chamber equipped with a circulating pump and with an oxygen sensor. Fish were starved for 1 wk prior to any respiration experiments (except when noted) and allowed to acclimate in the chamber 24–36 h. The respiration chambers were usually placed in the same tank as the fish, and fish readily swam into the chambers with little coaxing. The chambers were 89.9- and 68.6-L-Plexiglas rectangular boxes. A Kanwisher-type polarographic electrode, amplifier, and recorder system monitored the depletion of oxygen (Kanwisher 1959). These electrodes were calibrated with Winkler titrations, and with air-saturated and nitrogen-purged seawater as limits.

The chambers were set up as either flow-through or closed systems. Closed systems were used to monitor respiration rates down to very low oxygen tensions, and experiments were run with and without chemical filters that removed ammonia and urea. Open-system respirometry was used to examine respiration rates over 48-h periods at relatively constant, high-oxygen tensions (85–90% saturated). Both open and closed respiration measurements are interpreted as routine metabolic rates. Routine metabolic rate is defined as the rate of oxygen consumption during normal spontaneous activity for organisms in a postabsorbtive state and thermally acclimated (Brett and Groves 1978). This describes the condition of sablefish starved for 1 wk and unrestrained within the chambers.

Several control experiments were run to determine bacterial metabolism and bacterial scavenging of ammonia produced. There was no change in oxygen tension in a closed chamber over a 48-h period, and a chamber pulsed with ammonia equal to the maximum values seen in excretion experiments (84 mg/L) showed no change in the ammonia levels over 48 h. Therefore, we found no microbial interference either in the consumption of oxygen or in the scavenging of ammonia.

Excretion was evaluated by the production of ammonia in the respiration chambers; 18 urea determinations made on six fish showed urea to be less than 1% of the ammonia concentration with no detectable variation over time. Thus, monitoring of urea was discontinued. Both urea and ammonia were determined by methods outlined in Strickland and Parsons (1972). Excretion rates determined from ammonia assays are expressed as mg nitrogen excreted $\cdot kg^{-1} \cdot h^{-1}$.

In experiments where both oxygen consumption and nitrogen excretion were measured, oxygen-to-nitrogen ratios were calculated.

Results

Growth

Growth, ingestion rates, and conversion efficiencies for fish in all experiments are presented in Table 2. In the first experiment growth rates ranged from 0.066 to 0.085 kg gained per month. Conversion efficiencies were between 15

TABLE 3. Percent water, protein, and lipid of white muscle of *Anoplopoma fimbria* kept in the laboratory for 3 mo, experiments I and II), or collected from three sites in the Southern California Bight. Means are given with standard deviation (SD), coefficient of variation (C.V.), and sample size (*n*).

Site	Avg. weight, kg	Avg. length, mm	Water, %				Protein, %				Lipid, %			
			x	SD	C.V., %	*n*	*x*	SD	C.V., %	*n*	*x*	SD	C.V., %	*n*
Laboratory fish high rations	1.827	577	71.6	±1.8	3.0	7	13.9	±2.8	20.1	7	10.1	±2.6	26.0	7
Laboratory fish starved or low ration	1.850	570	70.3	±1.2	1.7	4	16.0	±3.0	18.8	4	9.5	±1.7	17.9	4
Scripps Canyon San Diego Trough	2.170	588	7.63	±5.7	7.5	15	12.8	±3.2	25.0	15	8.4	±3.0	37.5	13
San Clemente Canyon fish	1.480	527	76.9	±6.6	8.6	7	11.5	±3.2	27.8	7	5.6	±2.8	50.0	5
Santa Catalina Basin fish	1.284	514	84.2	±6.8	8.1	6	9.8	±3.4	34.7	6	5.2	±2.0	38.5	4

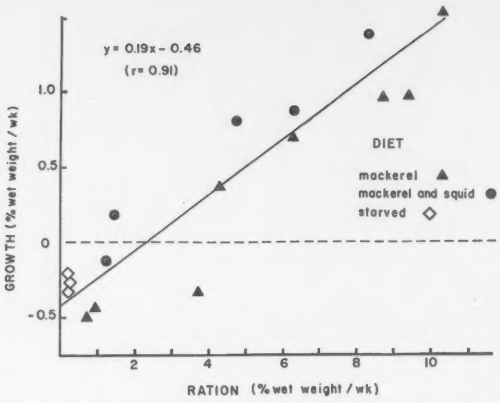

FIG. 2. Growth rate, expressed as % wet weight increase per week, is plotted against ration, expressed as of fish wet weight eaten per week for *A. fimbria* in experiments I, II, and III. Growth rates were evaluated after a minimum of 100 d on a specific diet. Ration level represents an average ingestion rate over the entire experimental period. A linear regression run on all values yield an *r*-value of 0.91.

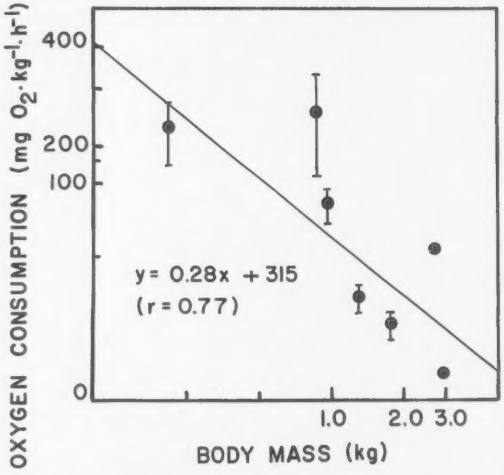

FIG. 3. Log–log plot of weight-specific oxygen consumption vs. wet body weight for *A. fimbria* at 8.0°C for fish starved for 1 wk prior to the experiment. Respiration measurements were made in an open respirometry system over 3–36 h with 5–22 measurements made on individual fish. Line represents linear regression curve fit to the equation $y = 0.28x + 315$.

and 20% for fish on a mixed diet of mackerel and squid. The average ingested food per week was very similar between fish, with very high standard deviations, indicating large variations in ingestion rates from week to week. The smallest fish initially (1.38 kg) showed the largest conversion efficiency and greatest growth rate. There was a general decrease in growth rate and conversion efficiency with increased size.

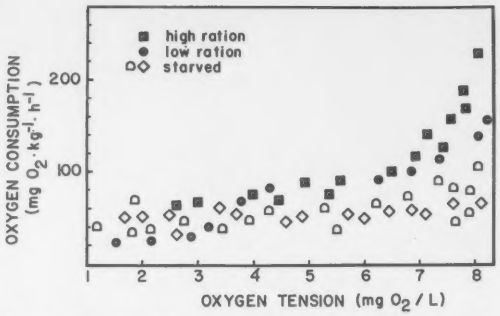

FIG. 4. Weight-specific oxygen consumption of *A. fimbria* vs. external oxygen tension for fish starved and fed in a closed respirometry chamber. All measurements were made at 8.0°C. High ration represents fish ingesting greater than 150 g food/wk, low ration represents fish ingesting less than 150 g food/wk.

In experiment II, fish on varying ration levels again showed large fluctuations in weekly ingestion rates, as indicated by the large standard deviations. Figure 1 illustrates the weekly ingested ration over the course of the experiment. All fish responded very similarly, and all fish varied their ingestion levels, even fish on limited rations. Conversion efficiencies were less for fish on mackerel diet alone ranging from 8 to 17%. Fish on restricted rations had roughly one-third the growth rate and one-third the conversion efficiency of fish on large rations.

In experiment III, fish ate a larger proportion of the ration presented, but had low growth rates and low conversion efficiencies on the synthetic high lipid diet. Fish on the filler diet also ate a large percentage of the ration presented. Fish on the filler diet lost weight more quickly than fish deprived of any food; starved fish in experiment II were quiescent most of the time compared to fish fed filler food which tended to have more short bursts of activity. Percent water, protein, and lipid of white muscle for laboratory and field sablefish is given in Table 3. In experiment I, two fish were killed after 100 d, and two fish were killed after 209 d. There was no significant difference between those four fish, indicating that changes from field-type muscle composition to laboratory-type composition occurs within the first 100 d of feeding in the laboratory. Laboratory fish, both fed and starved, had lower water content and higher protein and lipid contents than field fish.

A plot of growth vs. ration level for 17 laboratory sablefish (Fig. 2) in all three experiments exhibits a linear relationship between ration size and growth. Both ration and growth are expressed as percent wet weight of the fish. The maintenance ration, a theoretical ingestion level at which a fish neither gains nor loses weight, is about 2% of the wet body weight per week. Maximum ingestion levels for fish fed at 7- to 10-d intervals averaged over the 5- to 7-mo experiments is 10% of the wet body weight per week. The mixed diet of squid and mackerel yielded slightly higher growth rates per ration level than a diet of chopped mackerel alone.

RESPIRATION

Oxygen consumption vs. body weight for sablefish measured in an open respirometry system at 8.0°C (Fig. 3)

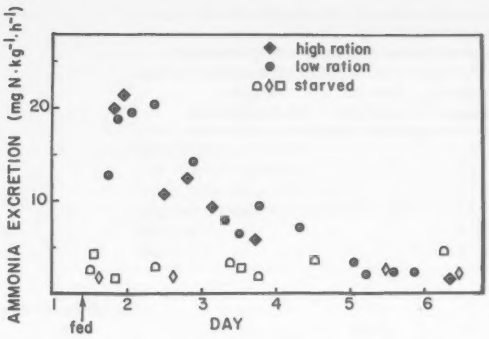

FIG. 5. Ammonia excretion over the course of a week for starved and fed *A. fimbria*. All measurements were made at 8.0°C, high ration represents fish ingesting over 150 g food/wk, and low ration represents fish ingesting less than 150 g food/wk. Fish were fed on the morning of day 1. Fish weights ranged from 1.0 to 1.9 kg.

showed a decrease in the weight-specific respiration rate with increase in size. Measurements represent an average oxygen consumption rate over 3- to 12-h experiments for fish in a postabsorptive state (1 wk after eating) and acclimated to the chamber for 24 h. The *b* exponent for the allometric equation $E_m = a\ M^b$ is 0.72 where E_m is oxygen consumption per hour. In Fig. 3, weight-specific respiration rate plotted against weight yields a slope of −0.28. The *b* value from the allometric equation is very similar to the theoretical value of 0.75 found for reptiles, mammals, and freshwater fish for mass-related changes in metabolic rate. The size range includes both mature and immature fish. This scaling relationship suggests that there are no ontogenetic changes in the metabolic rate during growth over the size range examined in the laboratory.

Oxygen consumption vs. external oxygen tension in closed respiration chambers at 10.0°C for starved and fed fish (experiment II) showed a decrease in the weight-specific respiration rate with a lowering of oxygen tension (Fig. 4). Starved fish, with already depressed respiration rates showed little change in oxygen consumption rates over a wide range of oxygen tensions. Fed fish showed a sharp decrease in respiration rates with a lowering in oxygen tension to rates comparable to the starved fish. In these closed-chamber experiments, ammonia was chemically scrubbed from the circulating water, thus the buildup of toxic waste products did not compound the effects seen in the closed system. Fish did not appear stressed at the conclusion of the closed experiments, but were quiescent.

Excretion

Ammonia excretion rates are plotted against day of the week for starved and fed sablefish (experiment II) in Fig. 5. Fed fish were fed the morning of day 1, and water samples were collected at 4- to 10-h intervals throughout the week in an open chamber. Starved fish showed a low nitrogen excretion rate that did not vary over the course of the week. Fed fish showed a peak in ammonia excretion 12−24 h after feeding. Nitrogen excretion rates remained elevated up to 4 d after feeding; however, by the end of the week excretion rates of fed fish were similar to those of starved fish. Patterns of nitrogen excretion suggest that a fish is not in a postabsorptive state for up to 5 d after feeding, thus allowing a week after feeding for all respiration experiments would remove food-processing costs from oxygen consumption measurements.

Muscle Composition

Sablefish maintained on a limited ration or starved in the laboratory have a higher muscle protein and lipid content than wild fish caught off southern California (Table 3). The variation between fish is much lower than for fish caught in the field as indicated by the lower coefficients of variation for the muscle composition parameters. Field fish from Scripps Canyon, San Diego Trough, and San Clemente Canyon all had very similar white muscle compositions. Scripps Canyon fish were used for comparisons to laboratory fish; five fish were killed and analyzed at the beginning of each of the three experiments. Fish from experiments I and II are represented in the laboratory fish. There was no significant difference between laboratory fish (Student's *t*-test, $P = 0.05$) on either full or partial/starved rations. Fish collected in Santa Catalina Basin showed the highest muscle water content and the lowest protein and lipid contents; the muscle characteristics of these fish varied significantly from other fish collected (Student's *t*-test, $P = 0.10$).

The muscle composition of wild vs. laboratory fish, the variation in ingestion rates (Fig. 1), and the extended period of elevated nitrogen excretion rates (Fig. 5) suggest that sablefish occurring off southern California are capable of surviving well on large, very infrequent meals. The laboratory evidence suggests the fish is physiologically capable of eating very infrequently, and in fact laboratory fish were not starved in the sense of catabolizing muscle protein by food deprivation of 4−5 mo.

Discussion

Food deprivation for a number of months does not result in starvation for *A. fimbria* maintained in the laboratory. *Anoplopoma fimbria* appear to be capable of a wide range of respiration, ingestion, and growth rates, and seem to thrive well on large, infrequent meals. Starvation in shallow-living fish such as plaice (*Pleuronectes platessa*) has been shown to result in a significant change in white muscle composition, with an increase in water content and a drop in protein and lipid content after 35 d without food (Jobling 1980). Sablefish held in the laboratory for 5 mo without food did not differ significantly in muscle composition from those fed weekly. The energy allocation of a fish ingesting large, infrequent meals has not been investigated previously and may hold valuable insights to feeding and energetics of very deep-living marine fishes.

Growth and Ingestion

Growth of laboratory *A. fimbria* varies with both size and composition of ration, and growth rates measured in the laboratory ranged from growth rates calculated from penned-reared and wild sablefish (Table 4) to four times that of known growth rates. Initial lengths of the fish suggest that the sable-

TABLE 4. Available growth rates and conversion efficiencies for pen-reared (Kennedy 1970) and wild-tagged (Pruter 1954) *Anoplopoma fimbria*.

Study	Initial weight, kg	Months observed	Gain per month, kg	Conversion efficiency, kg flesh/kg food
Penned-reared sablefish held off Nanaimo, Canada (Kennedy 1970)	0.35–1.90	18	0.11–0.15	0.11
Wild-tagged sablefish caught off Oregon (Pruter 1954)				
2-yr-old fish	0.69	12	0.033	—
3-yr-old fish	1.14	12	0.038	—
4-yr-old fish	1.69	12	0.042	—

TABLE 5. Energy budget for laboratory-reared *Anoplopoma fimbria* based on measurements of growth, respiration, and nitrogenous excretion. Values are expressed in joules per week, with percent of ingested calories in parentheses. All fish were held in the laboratory for 4 mo on a high lipid synthetic diet containing 6.26×10^3 per gram of food. Based on the composition of white muscle when the fish were sacrificed at the end of 4 mo, 4.31×10^3 J are needed to add 1 g of muscle tissue to fish.

Fish weight, kg	Avg. ingestion, kJ/wk	kJ/kg	Metabolism, kJ/wk	Growth, kJ/wk	Excretion, kJ/wk
0.250	247.9 (100%)	991.6	54.8 (22%)	151.1 (60%)	11.7 (4.7%)
0.880	371.8 (100%)	422.5	223.1 (60%)	119.7 (32%)	28.5 (8.0%)
2.780	929.5 (100%)	334.3	197.2 (21%)	95.0 (10%)	85.8 (9.2%)

fish used in the experiments were 3- to 4-yr-old fish, and probably sexually immature (Conway 1967). Generally, conversion efficiencies are higher for smaller fish on high ration levels and not necessarily associated with the highest growth rates (Huisman 1976). Smaller sablefish tend to show the highest conversion efficiencies, but not always the highest growth rates. Smaller fish typically devote a large percentage of energy to growth (Brett 1976), and this is seen in the energy budget of three sablefish ranging from 0.25 to 2.7 kg (Table 5). The wide range of growth rates seen in the laboratory helps explain the extremely wide variability in lengths for a given age-class of sablefish in the field. Pruter (1954) found that the fork length of a 2-yr-old fish caught off Oregon and aged by otoliths can range from 350 to 590 mm in fork length, the range for 3 yr-old fish is from 390 to 670 mm and the range for 4-yr-old fish from 440 to 720 mm. This range of sizes for a given age-class has also been encountered by Conway (1967) for sablefish collected off southern California. In the northern end of their range, sablefish spawns from December to April, with the peak months being January and February (Phillips 1969). The difficulty in aging field fish is complicated not only by the long spawning season, but also by the range of potential growth rates for this species. Changes in food availability both with season and with depth could result in variable growth rates for cohorts.

Ingestion rates of sablefish were extremely variable, even after the fish had been in the laboratory for several months. This variability in ingestion rates has two possible explanations. First, large marine fish, e.g. sablefish, may not be well suited for laboratory study. This seems unlikely because of the very high growth rates seen in the laboratory. However, fish in chemical contact with one another have very similar ingestion patterns (Fig. 1) suggesting a social aspect to their feeding behavior may be disrupted in the laboratory. Second, ingestion rates may be very variable because the periodicity of feeding in the field is even greater than 1 wk. Field fish may be feeding at irregular, infrequent intervals.

If indeed, sablefish feed very infrequently in the field, this would explain the lack of starvation stress after several months of food deprivation, as reflected in the similar muscle compositions of fed and starved fish. Smith (1978) measured very low in situ respiration rates for the abyssopelagic rattail, *Coryphaenoides armatus*, and estimated from neutral lipid stores that the animal had 189 d of energy stored in lipid reserves. Sablefish have an order of magnitude higher lipid content than the rattail, and estimating that 70% of the lipid is neutral (or triglycerides) based on several fractionations, field fish from Scripps Canyon had 163 d of energy stored in lipid reserves. This calculation was based on respiration rates measured on laboratory fish of the same size. Exercise and burst swimming activity are energetic costs not accounted for in the laboratory. Burst swimming can elevate metabolic rates two orders of magnitude (Webb 1975); while fish in the laboratory did show bursts of activity, they were confined to spaces so small that they could not accelerate to any speed. Until levels of activity of swimming ability can be estimated for field fish, it is impossible to estimate the added expense of exercise on the daily energy requirements and

TABLE 6. Growth expressed as percent wet weight on a given ration level for carp, brown trout, and *A. fimbria* of comparable size. All fish reared between 8 and 10°C with the exception of *A. fimbria* reared in surface-floating pens experiencing summer high temperatures of 18°C (Kennedy 1969).

Fish species	Growth, % wet wt·d^{-1}	Ration, %wet wt·d^{-1}	Reference
Carp (*Cyprinus carpio*)	1.3	2	Huisman (1976)
Carp (*Cyprinus carpio*)	2.2	4	Huisman (1976)
Brown trout (*Salmo gairdneri*)	1.1	2	Huisman (1976)
Sablefish (*Anoplopoma fimbria*)	0.3	2	This study (experiment I)
Sablefish	0.2	2	This study (experiment II)
Sablefish	0.2	2	Kennedy (1969)

growth of the fish.

RESPIRATION AND EXCRETION

Oxygen consumption rates were determined under constant temperature conditions, and there appeared to be two important factors influencing oxygen consumption in sablefish: body weight and external oxygen tension. There is an order of magnitude difference in the respiration rates of the smallest (0.25 kg) and largest (2.78 kg) fish (Fig. 3). Individual fish of varying sizes are able to survive under a wide range of external oxygen tensions. Starved fish have a very constant, low rate of oxygen consumption (40–80 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$) over a wide range of oxygen tensions. Fed fish decreased their rate of oxygen consumption with a decrease in oxygen tension from 235 to 62 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$. Environmental oxygen tensions encountered by sablefish off southern California range from 0.34 to 0.80 mg O_2/L at depths greater than 450 m in the various basins (Emory 1960). Oxygen tensions have been found as high as 2.0 mg O_2/L at a depth of 1300 m on a seasonal basis in Santa Catalina Basin (Smith and Laver 1981). Sablefish collected off southern California spend at least part of their time in colder and less-oxygenated water than provided by our study. Temperatures in the depth range where the laboratory fish were collected range from 3.5 to 5°C. Measurements made under lower oxygen tensions, and information on the change in respiration rates with lowering of temperature in fish (Brett and Glass 1973) suggests that in situ respiration rates would be much lower than those measured in the laboratory. Lowering the oxygen tension and respiration rates of the fish would lengthen the amount of time a fish could survive without feeding. Known in situ respiration rates for large (0.5–1.2 kg) macrourids at depths of 2750–3650 m at 3.5°C range from 3.9 to 5.3 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ (Smith and Hessler 1974; Smith 1978). The larger sablefish may respire at comparable rates at this low temperature; the lowest weight-specific respiration rate for a 2.78-kg fish at 8.0°C was 18.6 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$.

Carnivorous fish normally use protein as an energy source unless starved (Brett and Groves 1979), thus each milligram of nitrogen produced in the form of ammonia represents 6.25 mg of protein metabolized, based on an average nitrogen content of proteins of 16% (Houk and Ue 1974). Proteins metabolized by fish yield 20.1×10^3 J/g (Brett 1979). Energetic costs of growth (Table 5) are based on a final composition of sablefish muscle of 14.5% protein and 10% lipid. The calculated cost to add 1 g of muscle is 4.31×10^3 J. The 0.25-, 0.88-, and 2.78-kg fish gained 35, 28, and 22 g on 15, 7, and 6% rations, respectively.

A smaller proportion of the ingested energy can be accounted for in the largest fish, perhaps because of the development of energy-dense gonadal tissue or mucus production. In contrast, the smaller fish have 86 and 99% of the ingested energy accounted for in growth, metabolism, and nitrogen excretion. Feces from the sablefish were often a fine, flocculant material that was very difficult to collect quantitatively, and there seemed to be very little produced in small fish except for the expulsion of bones. In addition, the cost of food processing, the postprandial oxygen consumption (= specific dynamic action, Beamish 1974), was not accounted for in the energy budgets. From the patterns of nitrogen excretion, sablefish would most likely have small, long-term cost of food processing resulting in a slightly elevated oxygen consumption rate stretching over the period of several days.

In comparison to other fish energetics studies, the sablefish grow very slowly and have very low food to flesh conversion efficiencies. Carp and trout can convert over 50% of the ration wet weight into flesh under laboratory conditions (Huisman 1976) whereas the sablefish in the laboratory at best can convert 10–15% of ration wet weight to body weight (Table 6). The frequency and size of the meal plays an important role in conversion efficiencies and growth rates. By ingesting large, infrequent meals sablefish may grow very slowly, but is also able to survive well on a variable food supply. Energetics of sablefish collected off southern California may give some insight as to how very deep-living fish allocate energy when feeding on random, episodic bait falls.

Acknowledgments

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Lake Erie Oxygen; The Prehistoric Record

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DELORME, L. D. 1982. Lake Erie oxygen; the prehistoric record. Can. J. Fish. Aquat. Sci. 39: 1021–1029.

Periodic anoxia as a symptom of eutrophication has lasted for hundreds, maybe thousands, of years in the central basin of Lake Erie. Fossil ostracode remains in sediment cores show that a common species, *Candona caudata*, has been able to survive despite periodic anoxia because of its tolerance to low dissolved oxygen (as low as 2.3 mg/L at 16.5°C) and a short life cycle of weeks to several months. These qualities have enabled it to survive despite oxygen levels below 2.3 mg/L. Two other species, *Candona subtriangulata* and *Cytherissa lacustris*, that were expected in the sediment cores were not present. They were not able to cope with periodic low oxygen levels because of their requirement for higher dissolved oxygen (5.6 mg/L at 11.5°C, 3.0 mg/L at 12.8°C) and a life cycle of about 1 yr. This condition appears to have been common in the lower part of some of the sediment cores examined. A time-transgressive change in carbon concentration occurred in the surficial sediments of the central basin. A decrease in carbon started in the Sandusky basin around 4000 yr ago and gradually extended itself to the middle of the central basin by 1220 A.D. The loss of carbonate in the upper part of the sediment profile probably resulted from trapping of carbon dioxide, produced by the decomposition of organic material by oxidation and bacterial activity, in the hypolimnion.

Key words: Lake Erie, periodic anoxia, ostracodes, inorganic carbon, organic carbon

DELORME, L. D. 1982. Lake Erie oxygen; the prehistoric record. Can. J. Fish. Aquat. Sci. 39: 1021–1029.

Dans le bassin central du lac Erié, une anoxie périodique, symptomatique d'eutrophisation, a duré pendant des centaines, peut-être des milliers d'années. Des restes d'ostracodes fossiles présents dans des carottes de sédiments indiquent qu'une espèce commune, *Candona caudata*, a pu survivre en dépit de l'anoxie périodique, grâce à sa tolérance à une basse teneur en oxygène dissous (aussi faible que 2,3 mg/L à 16,5°C) et un cycle biologique court, variant de quelques semaines à plusieurs mois. Ces qualités ont permis à l'espèce de survivre à des niveaux d'oxygène inférieurs à 2,3 mg/L. Deux autres espèces, *Candona subtriangulata* et *Cytherissa lacustris*, qu'on s'attendait de trouver dans les carottes n'étaient pas présentes. A cause de besoins plus grands en oxygène dissous (5,6 mg/L à 11,5°C, 3,0 mg/L à 12,8°C) et un cycle biologique d'environ un an, ces deux espèces ne purent survivre aux bas niveaux périodiques d'oxygène. Cette condition semble commune à la partie inférieure de certaines carottes de sédiments examinées. Il se produisit dans les sédiments superficiels du bassin central un changement graduel dans le temps de teneur en carbone. Une diminution début dans le bassin Sandusky il y a environ 4 000 ans et se répandit pour atteindre le milieu du bassin central en l'an 1220 A.D. La perte de carbonates dans la partie supérieure du profil sédimentaire résulta probablement de l'emprisonnement dans l'hypolimnion du gaz carbonique produit par la décomposition du matériel organique par oxydation et action bactérienne.

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THE central basin of Lake Erie periodically experiences summer oxygen deficiencies. The tropholytic waters of this basin do not have the ability to oxidize all the carbon produced; consequently, organic carbon is stored in the sediments of the lake bottom. This excess productivity consumes oxygen which, by itself, is not serious, provided there is a constant source of oxygen, but thermal stratification curtails the flow of dissolved oxygen to the bottom layer of water. Temperature, oxidation of organic carbon, and thickness of the tropholytic zone are the major factors creating oxygen deficiency in the hypolimnion of the central basin.

The question being posed is how long has periodic oxygen deficiency been occurring in the central basin of Lake Erie?

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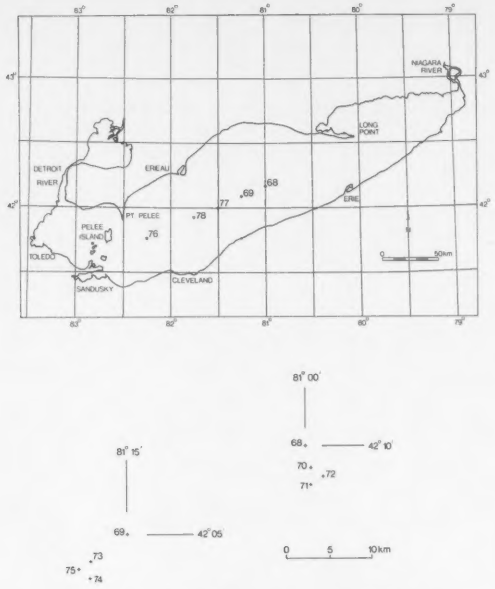

FIG. 1. Geographic location of cores from Lake Erie.

If near oxygenless conditions had existed for hundreds or thousands of years, there can be little doubt that overproduction would be a natural state and not solely related to man's activities. If overproduction is found to be a recent phenomenon, then man's activities can be considered as the cause of an accelerated aging process.

In the Lake Erie watershed, the oldest city is Detroit, Michigan, founded in 1701 (Delury 1978), and as such this date can be used as the reference datum between a natural and man-induced phenomenon. If oxygen deficiency had already been present prior to 1700, then the central basin would have been overproductive when the settlement was founded. If oxygen deficiency had not been established prior to 1700, then overproduction in the central basin could have been accelerated by cultural change.

Historical records on oxygen depletion for the central basin of Lake Erie extend back only to about 1929 (Dobson and Gilbertson 1972). Therefore, some alternate means of determining past oxygen conditions must be sought to extend the record to some period prior to the 1920s and 1700.

Some benthic organisms which are known to be sensitive to certain oxygen levels have existed in the lake for the past several thousand years as demonstrated by their fossil remains in the sediments (Benson and MacDonald 1963). Based on field collections from 6720 stations from lakes, ponds, and streams from across Canada, Delorme (1969, 1978) has collected autecological information relative to some 120 freshwater ostracode species. The present-day (1975) distribution in Lake Erie of seed shrimps (ostracodes) indicate a certain sensitivity to varying oxygen levels. Delorme (1978) has recorded three species in Lake Erie with oxygen needs above 2.3 mg/L.

Candona subtriangulata has a minimal tolerance requirement for dissolved oxygen of 5.6 mg/L at a bottom water temperature of 11.5°C (oxygen saturation of 50%). The modern distribution of the species includes Lakes Superior, Huron, Michigan, Ontario, and the eastern basin of Lake Erie. In Lake Superior the lowest oxygen saturation at which this species has been recovered is 77% (10.4 mg/L dissolved oxygen). In smaller Ontario lakes such as Lakes Muskoka and Joseph, Trout, Golden, Round, and Mazinaw Lakes, the percent oxygen saturation that *C. subtriangulata* is associated with varies from 50 to 106. Another important factor in the survival of this species is that its life cycle spans at least a year (Delorme 1978). This means that if the oxygen supply at the bottom of the lake decreases below the acceptable minimum tolerance limit, the species will not survive. If the oxygenless period is repeated over several years, no specimens will reach sexual maturity, no progeny will develop, and the species will become locally extinct.

Cytherissa lacustris survives in lakes whose bottom waters

TABLE 1. Coordinates, depth of water, and date collected of 11 cores from the central basin of Lake Erie.

Core	Latitude	Longitude	Depth of water (m)	Date collected	Station no.
68	42°10′59″	81°00′00″	22.9[c]	June 12, 1979	I-21[a]
69	42°05′29″	81°15′05″	23.8[c]	June 12, 1979	H-19[a]
70	42°09′36″	80°59′30″	22.0[d]	Aug. 1976	3A[b]
71	42°08′36″	80°59′30″	23.0[d]	"	3B[b]
72	42°09′06″	80°58′30″	23.2[d]	"	3C[b]
73	42°03′48″	81°18′12″	23.5[d]	"	4A[b]
74	42°02′48″	81°18′12″	23.5[d]	"	4B[b]
75	42°03′18″	81°19′12″	23.0[d]	"	4C[b]
76	41°44′01″	82°12′07″	18.2	June 13, 1979	D-11[a]
77	42°00′50″	81°31′05″	23.6[c]	June 14, 1979	G-17[a]
78	42°55′06″	81°43′00″	25.6	June 14, 1979	F-15[a]

[a]NWRI, Cruise Rep. 79-01-004.
[b]CCIW, Cruise Rep. 76-01-003.
[c]CCIW, Cruise Rep. 75-01-004.
[d]H. Wong, National Water Research Institute, CCIW, Burlington, Ont., personal communication.

TABLE 2. Summary of sedimentation rates.

Core	Level of *Ambrosia* increase (cm)	Sedimentation rate ($g \cdot cm^{-2} \cdot yr^{-1}$)	Time to deposit core
68[a]	—	—	—
69	3.2	0.009	—[b]
70	—	0.017[c]	1200
71	—	0.016[c]	1300
72	—	0.022[c]	1000
73	—	0.017[c]	570
74	—	0.024[c]	470
75	—	0.018[c]	550
76	4.3	0.011	—[b]
77	9.5	0.020	3200
78	11.0	0.020	3500

[a]Top of the core missing.
[b]Based on the assumption of a constant rate of sedimentation which may not be valid for the core.
[c]After Nriagu et al. (1976).

contain dissolved oxygen concentrations above 3.0 mg/L (temperature of 12.8°C, oxygen saturation of 27%). The modern distribution of this species includes the Great Lakes except the central and western basins of Lake Erie (Delorme 1978). In Lake Erie the species occurs in the shallow littoral zone at depths between 12 and 20 m where the oxygen concentration varies from 6.4 to 10.6 mg/L (oxygen saturation from 65 to 102%). In the Bay of Quinte the lowest oxygen values in association with *C. lacustris* were 5.2 to 9.1 mg/L (O_2 saturation of 48–92%). In Lake Winnipeg the species was recovered from bottom waters with 3.0 mg/L dissolved oxygen at an oxygen saturation of 27%, when the hypolimnion was just beginning to develop. *Cytherissa lacustris* also has a life cycle which spans a year (Delorme 1978). Presence of the species at the sediment–water interface is kept to a very low probability when dissolved oxygen falls below 3.0 mg/L and the near oxygenless condition is recurrent.

Candona caudata is found in bottom waters of lakes where the oxygen saturation is greater than 23% at 2.3 mg/L dissolved oxygen. The species occurs in all of the Great Lakes. *Candona caudata* is known to exist in the part of the central basin of Lake Erie that goes anoxic periodically (Delorme 1978). The species is present in the littoral area of the lake where the oxygen concentration gets as low as 6.8 mg/L (62% oxygen saturation). In the Bay of Quinte it is associated with oxygen values as low as 2.3 mg/L (23% oxygen saturation). Delorme (1978) has indicated that *C. caudata* has a life cycle which spans weeks to several months. This short life cycle assures several generations per year as eggs continue to hatch, but the nauplii survive only when oxygen levels are above the minimum level required. This allows the species to continue to reproduce itself until anoxia wipes it out again.

Taking current values of hypolimnetic temperatures of Lake Erie and given minimal oxygen saturation values for the three species, comparisons show that their minimal oxygen needs are barely met. From their data (Burns and Ross 1972, p. 98) the saturation values decrease from 37% (10.07°C, 4.29 mg/L) to less than 1% saturation (11.9°C, 0.05 mg/L)

TABLE 3. Distribution of ostracodes in core 68.

Depth (cm)	*Candona caudata*	*Candona* sp.	*Candona elliptica*	*Candona rawsoni*	*Cytherissa lacustris*	*Limnocythere friabilis*	*Physocypria pustulosa*
0–1.4		2			2		
1.4–2.7		2					
2.7–4.1	1	3					
4.1–5.4	2	2			2		
5.4–6.6	2	6					
6.6–7.6	6	25					
7.6–8.6	5	18					
8.6–10.0	6	34					
10.0–11.3	8	8	1				
11.3–12.5	3	5					
12.5–13.8	3	9					
13.8–15.0	8	12					
15.0–16.1	8	7		1			
16.1–17.3	10	10+					4
17.3–18.4	8	8+					
18.4–19.6	8	8+					
19.6–20.9	1	7	1				
20.9–22.3	10	10+					
22.3–23.3	7	7+				1	
23.3–24.5	3	8					
24.5–25.7	2	2					
25.7–26.9		3					
26.9–28.0	4	10					
28.0–29.2	3	5					
29.2–30.4	1	2					
30.4–31.5	2	4					
31.5–32.6	3	11					
32.6–33.9	7	12					
33.9–35.1	5	14					
35.1–36.3	3	12	1				
36.3–37.5	9	8					
37.5–38.7	2	6					
38.7–39.8		6					
39.8–41.0	1	1					
41.0–42.4							
42.4–43.4	6	7					
43.4–44.8	4	6		1			
44.8–46.0		8					
46.0–47.2	1	5					
47.2–48.3	3	14					
48.3–49.5	3	4					
50.7–51.8	3	4					
51.8–52.8	10	8					
52.8–54.0	7	9					
54.0–55.0	13	8					
60.9–62.0	2	9					
66.4–67.5	7	10					
71.9–73.0	4	5					
77.6–78.8	2	4					
83.2–84.4	1	3					
89.9–90.2	3						
94.7–95.8	5	9					
100.4–101.6		3					
106.2–107.2		4					
111.9–113.0	5	9					
117.6–118.6	1	7					
123.4–124.4		3					
128.8–129.9	1	1					
133.2–134.4	3	4					

TABLE 4. Distribution of ostracodes in core 70.

Depth (cm)	*Candona acuta*	*Candona caudata*	*Cypria ophthalmica*	*Cytherissa lacustris*	*Candona* sp.
0.0–1.2	2			4	6
1.2–2.2					
2.2–3.2		1			
3.2–4.2					3
4.2–5.3					
5.3–6.3					2
8.3–9.4					
9.4–10.5					1
10.5–11.7		1			
15.0–16.0					
16.0–17.1					4
17.1–18.2		2	1		6
18.2–19.3					4
19.3–20.4			1		16
20.4–21.5		4	1		11

TABLE 5. Distribution of ostracodes in core 71.

Depth (cm)	*Candona caudata*	*Candona rawsoni*	*Candona* sp.	*Cypria ophthalmica*	*Cytherissa lacustris*	*Limnocythere friabilis*
1.0–2.0						
2.0–3.3					2	
3.3–4.4			1			
4.4–5.1						
5.1–6.1			2			
6.1–7.1						
7.1–8.0						
8.0–9.0			1			
9.0–9.9			1			
9.9–11.1			5			
11.1–12.0			4			1
12.0–13.1	21		5	2		
13.1–14.0	50	17		3		1
14.0–15.1	8	2		1		
15.1–16.2	10	3				
16.2–17.3	2		2			1
17.3–18.4	1	3	2	1		
18.4–19.4	6					
19.4–20.6	1		10			1

which would kill off the three species if present. This would come about by decreasing the oxygen levels at a given temperature to the point below which the species could not survive. The order in which the species would die off are *Candona subtriangulata* (5.6 mg/L), *Cytherissa lacustris* (3.0 mg/L), and *Candona caudata* (2.3 mg/L).

To examine the fluctuations in oxygen-sensitive ostracode populations over time, this study will look at the presence–absence of fossil ostracodes in several cores from the central basin.

Methods

Collection and Sampling of Cores

A total of 11 cores was examined. Five cores (numbered 68, 69, 76, 77, and 78) were collected along the central axis of the central basin of Lake Erie during a June 1979 cruise of the CSS *Limnos* (Fig. 1). Six additional cores (70–75) collected in 1976 by Nriagu et al. (1979) are included, because they are located close to two of the 1979 cores and also provide additional information on sedimentation rates. Table 1 provides detailed coordinates, depth of water, and collection time for each core investigated.

Cores were obtained with a Benthos corer, X-rayed, subsectioned, and freeze-dried prior to fossil extraction. Prior to slicing the core, the outer smeared portion was removed leaving a diameter of 5 cm or a volume of about 20 cm^3. The sample thickness was about 1 cm, with every centimetre sampled. The samples were weighed, freeze-dried, and weighed again. Calculations of porosity, sediment volume, cumulative dry weight, and length of core are given in Delorme (unpublished manuscript). The dry sediment was passed through a set of sieves (0.841 and 0.250 mm). All adult ostracode shells were retained on the 0.250-mm mesh from which all shells were picked and reported as shells per sample. Immature shells or molts were not identified to the species level because of similarity of shapes between species in one genus.

The X-radiographs of cores 68 and 76 show well-defined laminations, while those of cores 69, 77, and 78 show only faint laminations.

Results

Chronology

The primary methods for determining when certain events have taken place in the past have been either by ^{210}Pb dating or palynology. As indicated earlier in this paper, historical records have not registered the beginning of periodic anoxia in the central basin; therefore, oxygen conditions inferred from the presence or absence of certain ostracodes must be tied down to a chronology to determine when the events took place.

McAndrews and Boyko (1972) have placed the beginning of large-scale agriculture in the Great Lakes basin at 1850, which is substantiated by pollen profiles showing an increase in *Ambrosia* pollen concentration in Lake Erie. Kemp et al. (1974) had difficulty objectively locating the *Ambrosia* horizon in the pollen profiles of Lake Erie. Esterby and El-Shaarawi (1981a, b) have discussed the use of the likelihood method as an objective approach to determine the point of change in a profile. As the depth that corresponds exactly to 1850 is not clearly apparent, the likelihood method was used to determine when the influx in *Ambrosia* pollen started (Table 2).

Distribution of Ostracodes

Ostracode shells do occur in the upper metre of the cores 68, 70, 71, 72, and the bottom part of core 76 collected along the central axis of Lake Erie, with *Candona caudata* appearing as the most successful. The cores are devoid of the ostracode species, *Candona subtriangulata* and *Cytherissa lacustris*.

TABLE 6. Distribution of ostracodes in core 72.

Depth (cm)	*Candona caudata*	*Candona* sp.	*Cyprinotus* sp.	*Cytherissa lacustris*
0.0–0.7				2
0.7–1.9		1		
1.9–2.8				
2.8–3.9		1		
3.9–5.0				
5.0–6.1		4		
6.1–7.1				2
7.1–8.2	1	4		
8.2–9.3		2		
9.3–10.3				
10.3–11.4		1		
11.4–12.6		1		
12.6–14.0				
14.0–15.1		3	1	
15.1–16.3		3		
16.3–17.7				
17.7–18.8			1	
18.8–20.0	1	5		
20.0–21.3		4		
21.3–22.3		6		

Candona caudata is the only mature ostracode species occurring in core 68 in any significant number (Table 3). The restricted occurrence of ostracode species in this core is similar to that reported by Delorme (1978) for Lake Erie, with live specimens of only *Candona caudata* being recovered from the central basin. Mature specimens of *Candona subtriangulata* were not recovered. Determination of the *Ambrosia* horizon for core 68 places the 1850 date at a residual depth of 6.6 cm (note top of core missing), allowing one to conclude that the absence of *Candona subtriangulata* and *Cytherissa lacustris* suggests that a near oxygenless period had been already established prior to 1850.

Cores 70–72 contain ostracode shells intermittently (Tables 4, 5, 6). The predominant species is *Candona caudata* for cores 70 and 71, while core 72 contains few adult specimens. *Cypria ophthalmica* is present in the lower parts of core 70 and 71, but is absent in cores 68 and 72; it is one of few freshwater ostracodes that can live in anaerobic water. *Candona rawsoni* is present in core 71 at a depth of 13.1–18.4 cm. This ostracode has been recovered alive from other habitats with a dissolved oxygen concentration as low as 0.1 mg/L (Delorme unpublished data). Cores 70–72 do not contain *Candona subtriangulata* or *Cytherissa lacustris* indicating, for the length of core recovered, that oxygen levels were below 3.0 mg/L at least 1200, 1300, and 1000 yr ago, respectively (Table 2), except near the surface where *Cytherissa lacustris* occurs.

TABLE 7. Distribution of ostracodes in core 76.

Depth (cm)	*Candona caudata*	*Candona rawsoni*	*Candona* sp.	*Cypria ophthalmica*	*Limnocythere* sp.	Depth (cm)	*Candona caudata*	*Candona rawsoni*	*Candona* sp.	*Cypria ophthalmica*	*Cytherissa lacustris*	*Limnocythere* sp.
63.8–64.9						94.1–95.4	3	3	9			
64.9–66.1			2			95.4–96.5	4	3	13	1		
66.1–67.2	3	2	12			96.5–97.7	9	9	11	2		1
67.2–68.4	15	1	14			97.7–99.0	9	3	12	3		1
68.4–69.4	6	2	2			99.0–100.3	5	1	10	1	1	
69.4–70.5	8	2	4	1		100.3–101.6	8		7	1		1
70.5–71.7	2		1			101.6–102.5	4	1	9	3		
71.7–72.9	6	7	15			102.5–103.5	6	3	10	5		3
72.9–74.1	9	5	12			103.5–104.7	9	1		5		1
74.1–75.3	4		20			104.7–105.7	6	3	12	5		
75.3–76.2	9	3	11	3	1	105.7–107.0	5	3	1			
76.2–77.4	1		18			107.0–107.9	4		5			
77.4–78.7	9	3	9	1	1	107.9–109.0	4		11	3		1
78.7–79.8	15	7	2		2	109.0–110.3	3		8	1		1
79.8–80.9	10	2	6			110.3–111.4	6		3			
80.9–82.0	1		4			111.4–112.4	3		6	1	1	1
82.0–83.2	13	10	7			112.4–113.4	4	1	6			1
83.2–84.4	13	7	14	1		113.4–114.6	2		4			
84.4–85.7	6		2	1		114.6–115.8			4			
85.7–87.0	10	7	3			115.8–117.1	2	1	6			
87.0–88.1	1		6			117.1–118.2	9		8	1	2	
88.1–89.5	11	7	1			118.2–119.5		2	5			
89.5–90.6	14	3	2	1		119.5–120.6		3	5			
90.6–91.7	5	4	11		1	120.6–121.7	5	9	6			
91.7–92.9	1	1	11			121.7–122.6	4	2	4			
92.9–94.1	1	4	5			122.6–123.7	13		1			

TABLE 8. Summary of inorganic and organic carbon changes.

Core	Depth at which carbon change occurs (cm)	Avg., above the carbon break (mg g dry wt^{-1})		Avg., below the carbon break (mg g dry wt^{-1})	
		Carbon	$CaCO_3$	Carbon	$CaCO_3$
68	6.0[a]	114	19	254	119
69	>114.5	144	26	?	?
70	14.5	117	23	211	75
71	8.5	67	45	78	137
72	15.7	121	21	234	97
76	66.7	199	48	244	108
77	>130.2	125	21	?	?
78	>147.9	122	14	?	?

[a]Top of the core missing, actual depth not represented.

Cores 69, 73–75, 77, and 78 did not contain ostracode shells; core 76 is without shells in the upper 65 cm of sediment, although the remainder of the core down to 129 cm contains ostracode shells in reasonable abundance (Table 7). Next to *Candona caudata*, *Candona rawsoni* is the second most-abundant species in the fossil-bearing zone, occurring in 70% of the samples. *Cypria ophthalmica* occurs in 33% of the samples and is concentrated between 95 and 106 cm, the remaining 17% occurring intermittently in the core above 95 cm and below 106 cm. The combination *Candona caudata*, *Candona rawsoni*, and *Cypria ophthalmica* is the same that was recovered from core 71, but at a shallower depth. Core 76 is devoid of *C. subtriangulata*, and *C. lacustris* is rare between depths of 65 and 128.5 cm suggesting oxygen levels below 3.0 mg/L for short periods prior to 4030 yr ago.

The profile presented by the cores through the central axis of the central basin of Lake Erie is one of inconsistent presence of ostracode shells. Most striking is the absence of calcitic shells in cores 69, 73–75, 77, and 78. The extremities of the profile, cores 68, 70–72, and 76 do show the presence of shells, although the upper portion of core 76 is more like the central part of the profile and the lower portion more like the cluster of cores at the opposite end.

None of the 11 cores studied penetrated the low–high oxygen boundary. This is based on the premise that those ostracode species intolerant of less than 3.0 mg/L oxygen were not recovered from any of the cores (Table 2), even though depths equivalent to 1000s of years deposition were examined.

Delorme (1978) has noted that based on their oxygen requirements the three ostracode species *Candona caudata*, *Candona subtriangulata*, and *Cytherissa lacustris* should not be living in Lake Erie, and that the major difference between *C. caudata* and the other two species is its short life cycle, which allows *C. caudata* to propagate itself although killed off temporarily by anoxia. The other two species have become locally extinct in the central basin, presumably because repetitive low oxygen levels year after year has not allowed them to reach sexual maturity.

CARBON ANALYSES

A systematic search for calcitic shells in the sediments revealed some cores contained shells while others were devoid of them. Two scenarios are possible to explain the absence of shells. First, the habitat may have been inhospitable for ostracodes. Take, for example, the absence of shells in the top centimetre of cores 69, and 73–78. The 1975 survey of ostracodes (Delorme 1978) indicated shells as well as live specimens were present at these sites. This would indicate the habitat did support an ostracode population. The second scenario would be the habitat did support an ostracode population, but when the animal died the calcitic shells dissolved. The loss of calcium carbonate to the water in the form of bicarbonate is an anomalous situation for the central basin of Lake Erie when one considers the loading of 170–280 mg/L $CaCO_3$ from streams into the littoral water mass (100–125 mg/L $CaCO_3$). The source of CO_3 is from Paleozoic carbonates on which the basin is located. The loss of carbonate from both solution and solid phase appears to be related to decreases in pH during the development of the hypolimnion and to fall overturn in the central basin. During this time, the pH of the water decreases to less than 8.3 as a result of the accumulation of CO_2 and a decrease in temperature (7.4, Burns and Ross 1972; Burns et al. 1976) so the bottom water becomes undersaturated with respect to $CaCO_3$. The calcitic shells are then taken into solution when the ostracode dies. The only successful species, *Candona caudata*, can tolerate a minimal pH of 5.2 when it is present at the sediment–water interface.

Absence of fossil shells coincides with a diminished inorganic carbon content in all of the cores (Fig. 2–6). Kemp et al. (1976) and Thomas and Jaquet (1976) have recorded that inorganic carbon is significantly lower in the younger sediments in the central basin. There is a reduced concentration (range of 19 to 48 mg $CaCO_3$/g dry wt) of calcium carbonate remaining in the top portion of the cores, as compared to a higher amount of carbonate (range of 75–137 mg $CaCO_3$/g dry wt) further down the cores (Table 8). The separation between the two concentrations is very distinct in cores 68, 70–72, 76. The break does not occur in cores 69, 73–75, 77, 78 where it is presumed to be stratigraphically lower because values are all in the lower range (14 to 26 mg $CaCO_3$/g dry wt).

There are a number of ways in which carbonates can be decreased in concentration in the tropholytic zone. The major mechanism is to lower the pH below the carbonate–

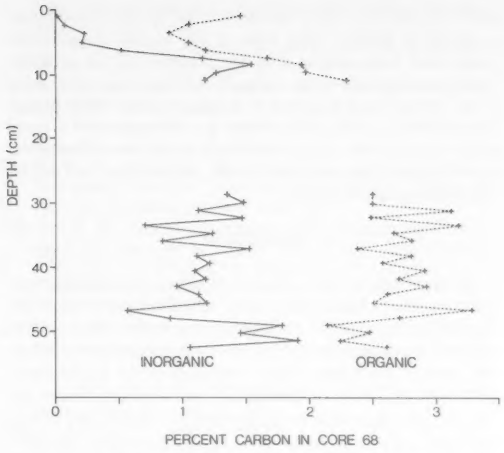

FIG. 2. Percent carbon by weight in core 68.

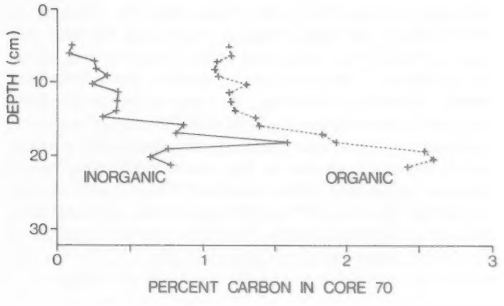

FIG. 3. Percent carbon by weight in core 70.

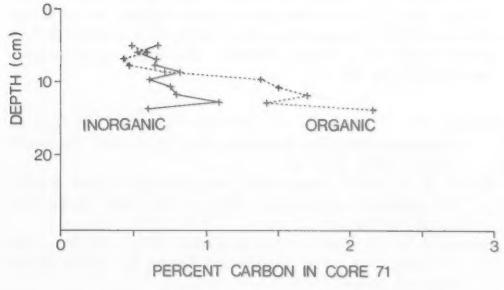

FIG. 4. Percent carbon by weight in core 71.

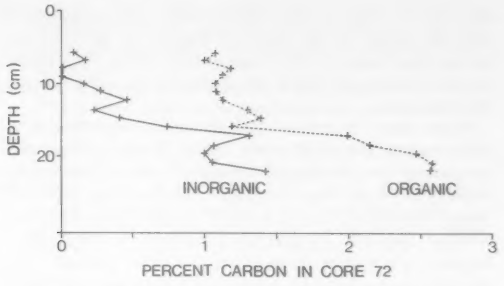

FIG. 5. Percent carbon by weight in core 72.

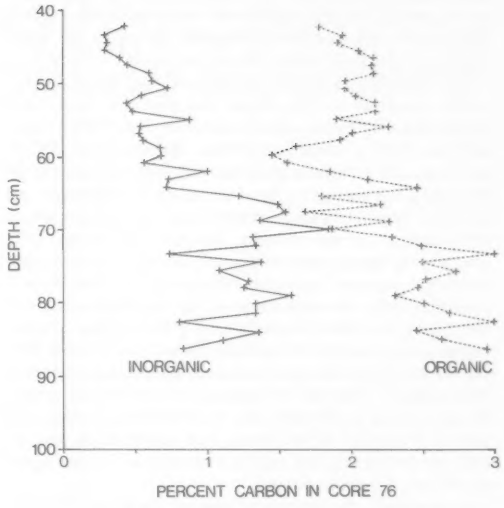

FIG. 6. Percent carbon by weight in core 76.

bicarbonate fence of 8.3, by allowing free carbon dioxide to combine with water to form carbonic acid. The acid in turn dissolves particulate carbonates and dissociates carbonate ions to form bicarbonates. The bicarbonates remain stable only in the presence of free carbon dioxide.

The major sources of carbon dioxide in the zone of decomposition are respiration by animals and plants, bacterial decomposition of organic matter, and the oxidation of organic substances. In unmixed deep waters, bicarbonates and free carbon dioxide are increased, while oxygen may be nearly or completely depleted; the pH is decreased. When oxygen levels go below 1 mg/L, oxidation ceases and reduction takes over; decomposition of organic matter is by anaerobic bacteria producing methane and carbon dioxide.

Simultaneous with the decrease of inorganic carbon, there is a decrease in organic carbon concentration from averages of 236 to 135 mg C/g dry wt (Fig. 2–6), a decrease of 43% (core 71 not included in the average because of anomalously low values). If one assumes a near-constant rate of organic production, then the loss of organic carbon must be accounted for. Erosion or nondeposition in the area of the cores is a possible explanation. However, based on the sediment texture and uniform distribution of organic silty clays, there is little indication of change in the process of deposition. Similarly, deforestation around 1850 may have diluted organic carbon by increasing mineral matter, but could not have been respon-

sible for the "carbon break" because there was no change in sediment texture at the *Ambrosia* horizon. In any case the carbon break which is time transgressive (Table 7) is below the rise in *Ambrosia* pollen, which also discounts the effect of deforestation.

What caused the increase in carbon dioxide production to define the carbon break in the cores? If one assumes that productivity has not changed significantly at any place in the trophogenic zone, then respiration from primary and secondary production can be assumed to have been relatively constant. Similarly, the generation of carbon dioxide by aerobic bacterial decomposition would have been constant. Carbon dioxide produced by anaerobic bacterial decomposition would have increased when the hypolimnion went anoxic. Oxidation of organic matter is a year-round process. The major requirement is that a net accumulation of organic carbon be present in the basin. Burns and Ross (1972, p. 110) have shown that oxidation of organic carbon in the hypolimnion is the major source of carbon dioxide.

The Sandusky basin, with its semi-enclosed physiography, would appear to be one of the first places to have a net accumulation of organic matter to oxidize. Carr (1962), Burns and Ross (1972), Great Lakes Water Quality Board (1975), and Burns (1976) indeed show that the Sandusky basin is the first area each summer to have an anoxic hypolimnion, and that this oxygen deficiency spreads eastward with the season until disrupted by fall overturn. That is to say, oxygen deficiency in the hypolimnion is currently time transgressive eastward on a seasonal basis and is likely to have been so on a historical basis. An examination of the residual organic carbon below the carbon break reveals a diminishing concentration towards the east in the basin from cores 76 to 68. This fact combined with the time-transgressive nature of the carbon break indicates that the development of hypolimnetic anoxia for one season recapitulates the development of anoxia for part of the history of the basin. The carbon break and the subsequent diminution in organic and inorganic carbon signal the advent of periodic anoxia.

In summary, the absence of calcitic shells in Lake Erie cores could be the result of an inhospitable habitat. However, the 1975 benthic survey shows ostracodes did exist. This then means the shells were dissolved. Loss of carbonates in the tropholytic zone, when the loading is sufficient to indicate their presence, is theoretically a function of chemical nonequilibrium, with the continued presence of carbon dioxide playing the major role. The absence of shells coincides with diminished carbonates in the upper portion of the sedimentary deposit in the central basin. The sources of carbon dioxide are respiration by plants and animals, decomposition of organic matter by aerobic and anaerobic bacteria, and by oxidation. An indication that organic carbon is the primary source of carbon dioxide is the simultaneous decrease in organic and inorganic carbon in the sediments. The decrease is not a product of erosion of organic matter or of deforestation in the drainage basin. The major source of carbon dioxide appears to be the oxidation of organic carbon in the hypolimnion. A shallow basin with a net accumulation of organic carbon and the development of a hypolimnion provides an ideal situation for producing carbon dioxide. The carbon break in the cores represents the initiation and continuance of periodic hypolimnetic anoxia in the central basin as the process moved from the Sandusky basin into the central part of the basin over a period of 4000 yr. The start of this anoxic phenomenon could well have started after the "erosion of the southern outlets of Nipissing Great Lakes II" which lowered the water levels of the Great Lakes to a minimum about 4000 yr ago (Prest 1970, p. 731). Sly (1976, p. 359) indicates a rapid jump of 8 m in the water level which would have allowed the hypolimnion to be developed in the summer time and not be disturbed by wind activity.

Discussion

Several authors have alluded to substantial degradation, either locally or basin-wide, of the central basin prior to 1850. Sly (1976) has stated "... [It] may be assumed that localized degradation of the lake waters [Erie] was apparent even before the 1850's." He further stated "Although evidence of reliable lake-wide dissolved oxygen data is not available before the 1920's, it is reasonable to suggest that the western and central basins of Lake Erie were already highly productive (in terms of primary biomass) even before European settlement and that oxygen depletion rates in the early part of this century were similar to the early records." Leach and Nepszy (1976) have also stressed this point, "Lake Erie, by virtue of its shallow depth and fertile drainage basin, was the most productive of the Great Lakes long before European man inhabited its shores." The conclusions arrived at above have been through subjective reasoning. The use of ostracode shells preserved in the sediments as well as the absence of shells and carbonates in the surface sediments has shown that periodic anoxia has been present in the central basin long before European settlement in this watershed. The calculations carried out by Charlton (1979, 1980) indicate that there has been little or no long-term trend of changing oxygen depletion in the central basin based on historical data (1929–70). His conclusions are supported by the results of this study.

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Habitat and Food Segregation of Dwarf and Normal Arctic Charr[1] (*Salvelinus alpinus*) from Vangsvatnet Lake, Western Norway

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HINDAR, K., AND B. JONSSON. 1982. Habitat and food segregation of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet Lake, western Norway. Can. J. Fish. Aquat. Sci. 39: 1030–1045.

The aim of the present study was to test possible habitat and food segregation between two charr morphs in Vangsvatnet Lake. The charr population of Vangsvatnet consists of one pale phenotype with parr marks along the flanks and poorly developed spawning coloration (dwarf charr), and another phenotype with silvery flanks in nonbreeding condition and bright red spawning colors (normal charr). The habitus of the two morphs indicated that they were adapted to different niches during the growth season. The analyses of distribution and food showed that there was marked habitat and food segregation between the two morphs during summer, when dwarf charr dwelled deep-benthic and normal charr roamed in the limnetic zone. The segregation broke down in periods of food abundance, indicating that the habitat segregation was due to intraspecific competition for food. A comparison of charr morphs of Vangsvatnet with the nearby Lønavatnet Lake suggested that the number of charr morphs is adapted to local environmental conditions, among which lake morphology, food availability, and other fish species are important. We hypothesize that the number of charr morphs within a locality depends on the number of available niches during the growth season.

Key words: polymorphism, camouflage, distribution, ontogeny, intra- and inter-specific competition

HINDAR, K., AND B. JONSSON. 1982. Habitat and food segregation of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet Lake, western Norway. Can. J. Fish. Aquat. Sci. 39: 1030–1045.

Le but de la présente étude est de vérifier la possibilité d'une ségrégation quant à l'habitat et à la nourriture de deux formes d'ombles chevaliers dans le lac Vangsvatnet. La population de ce lac est constituée par un phénotype pâle, avec marques de tacon sur les flancs et une livrée nuptiale mal formée (ombles nains), et un autre phénotype avec flancs argentés en condition normale et une coloration rouge brillant au moment de la reproduction (ombles normaux). L'apparence des deux formes indique que, durant la saison de croissance, elles sont adaptées à différentes niches. La distribution et la nourriture de ces formes indiquent qu'en été, il y a ségrégation prononcée quant à l'habitat et à la nourriture : la forme naine habite la zone profonde-benthique, alors que la forme normale va et vient dans la zone limnétique. En périodes d'abondance de nourriture, cette ségrégation disparaît, signe que la choix de l'habitat est le résultat d'une compétition intraspécifique pour la nourriture. Une comparaison des formes d'ombles du lac Vangsvatnet avec celles du lac Lønavatnet donne à penser que le nombre de formes d'ombles dépend des conditions ambiantes locales, parmi lesquelles la morphologie du lac, la disponibilité de la nourriture et les autres espèces de poissons sont importantes. Nous avançons l'hypothèse que le nombre de formes d'ombles dans une localité donnée est fonction du nombre de niches disponibles pendant la saison de croissance.

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[1]In this paper the spelling of the word charr differs from that (char) used in *A list of Common and Scientific Names from the United States and Canada*, by the American Fisheries Society, and is preferred by the authors.

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SYMPATRIC forms of landlocked Arctic charr (*Salvelinus alpinus*) occur throughout the geographic range of this fish (Behnke 1980). In deep lakes Arctic charr often occur in three forms: a deep-water dwarf form, a littoral or pelagic normal form, and a predatory form (Table 1). The phenotypical and ecological differences between the charr forms are profound, and several authors consider them to be sibling species (e.g. Svärdson 1961; Nilsson and Filipsson 1971; Nyman 1972; Henricsson and Nyman 1976; Klemetsen and Grotnes 1980).

TABLE 1. Characteristics of sympatric charr (*Salvelinus alpinus*) forms in deep lakes. The table is based on literature from Scandinavian (Nilsson 1955; Nilsson and Filipsson 1971; Nordeng 1961; Aass 1968; Filipsson and Svärdson 1976; Klemetsen and Grotnes 1980), Alpine (Haempel 1924; Reisinger 1953; Dörfel 1974, Brenner 1980), and Icelandic localities (Fridriksson 1939; Frost 1965).

	Dwarf form	Normal form	Predatory form
Habitat	Deep-benthic or deep-pelagic	Pelagic or littoral	Pelagic or benthic in all depth strata
Food	Profundal zoobenthos or zooplankton	Limnetic zooplankton, littoral and surface insects, littoral crustaceans and mollusks	Fish
Flesh color	White or pink	Pink or red	Pink
Size at maturity	12–27 cm	20–55 cm	35–70 cm
Coloration	Pale or dark, often parr marks; dull spawning colors	Silvery; bright red spawning colors	Pale, silvery, or dark; orange or bright red spawning colors

Other authors consider the charr forms to be phenotypes of a polymorphic species (e.g. Reisinger 1953; Savvaitova 1961, 1973; Skreslet 1973; Balon 1979, 1980). Nordeng (1982) has now demonstrated through rearing and transplantation experiments that different charr forms may be siblings.

Rearing of Arctic charr from Vangsvatnet Lake has shown this population to split into two phenotypes (Nordeng personal communication): one maturing sexually in the parr stage (dwarf charr), the other having a shift in shape and coloration before maturing sexually (normal charr). Our hypothesis was that these morphs segregate ecologically in the lake, parr and dwarfs being confined to deeper and more often benthic areas than normal charr. Thus the behavior of the two morphs should be ecologically equivalent to that proposed by Svärdson (1976) for sibling species of charr. Further we hypothesized that the segregation between the charr morphs is interactive, i.e. pronounced when food is scarce, and broken down in periods of food abundance. This we tested in a field study by examining possible habitat and food segregation throughout the year between the two charr morphs in Vangsvatnet Lake. Finally we focus on the connection between polymorphic charr populations and heterogeneous environments.

Study Area

Vangsvatnet Lake (60°37′N, 6°22′E) is situated in the Voss river system, western Norway, 46 m above sea level. The climate at Voss is semioceanic, mean air temperature in July is ~16°C and in January ~−5°C. The average yearly precipitation is about 1200 mm. Water level fluctuations, usually short term, are characteristic for the Voss river system (Matzow et al. 1976). These are related to snow melting in the spring and heavy precipitation, especially during autumn.

The configuration and morphometric parameters of Vangsvatnet Lake are given in Fig. 1. Vangsvatnet consists of two basins: an upper basin with a maximum depth of 60 m, and a lower basin, maximum depth 45 m, divided by a narrow sound, 12 m deep.

Vangsvatnet is dimictic and appears to be in an oligo-meso-trophic phase (Faafeng et al. 1979). In summer the surface temperature may reach 20°C; at the depth of 20 m it reaches 10–12°C. The thermocline is poorly developed. At the greatest depths of the two basins the temperature may vary between 2 and 7°C throughout the year. The lake, which is usually ice-covered from December to April, is well oxygenated, the upper water masses being always 100% saturated. Towards the end of the stagnation periods the oxygen saturation may decrease to about 70% in the deeper parts of the lake.

The substratum from the shoreline to about a 1.5-m depth consists of gravel and stones. A macrovegetation (isoetids and elodeids) is developed between a 1.5- and 5-m depth, except for the steepest gradients, where gravel and stones occur down to 15–20 m. In the deeper parts the sediments may be characterized as dy-gyttja.

Because of higher organic contents of the sediment, the bottom fauna — especially chironomids of the tribe Chironomini — is richer in the upper basin (cf. Matzow et al. 1976). The density of zooplankton is somewhat higher in the upper basin (Fig. 2). Dominant species are the cladocerans *Daphnia longispina* and *Bosmina longispina* and the copepods *Cyclops abyssorum* and *C. scutifer*.

Besides resident Arctic charr, Vangsvatnet supports populations of anadromous and resident brown trout (*Salmo trutta*), anadromous Atlantic salmon (*S. salar*), catadromous eel (*Anguilla anguilla*), and resident threespine stickleback (*Gasterosteus aculeatus*). Arctic charr are the numerically dominant species in the salmonid community, outnumbering trout three- to four-fold. However, trout occupy the littoral zone and the upper 1–5 m of the pelagic zone throughout the year. Trout feed mainly on insect larvae, surface insects, and zooplankton; however, sexually mature sea trout may feed on charr in the upper water masses in August–October. Atlantic salmon parr occur in small numbers along the bottom of Vangsvatnet, mainly at a depth of 5–15 m. Their food

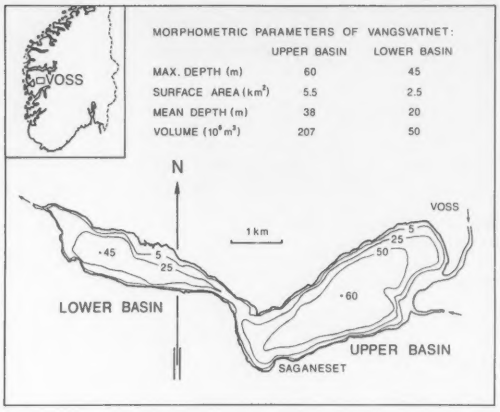

FIG. 1. Location of study area and morphometric parameters of Vangsvatnet Lake, western Norway.

consists of insect larvae and zooplankton.

Arctic charr is caught by local fishermen with bottom nets in spring and autumn, beach seines during the spawning time, and hook and line through the ice in winter. All methods catch predominantly charr with body lengths larger than 25 cm. Total catches amount to at least 6 t a year.

Methods

During the period May 1977–June 1979, we caught a total of 4359 charr (Table 2). Sampling was carried out by bottom nets, floating nets, beach seines, and bottom trawl of the push-net type. We placed the bottom nets (1.80 m × 25 m, mesh sizes 18–52 mm) in chains with mixed mesh sizes at least two nights each month from the shoreline to the greatest depths of each of the two lake basins (Fig. 3). Floating nets (5 m × 25 m, mesh sizes 16–45 mm) were used in chains

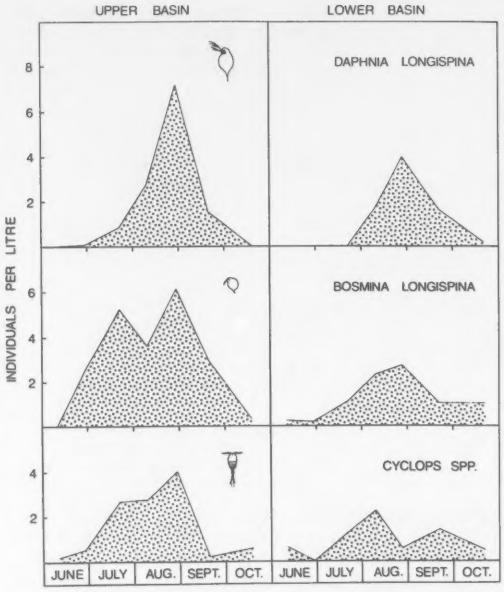

FIG. 2. Density of *Daphnia longispina*, *Bosmina longispina*, and *Cyclops* spp. (*C. abyssorum* and *C. scutifer*, adults and copepodid stages IV–V) in the two basins of Vangsvatnet Lake during June–October 1977. Data are based on mixed samples taken with a 3-L-plankton sampler at the depths 1, 2, 4, 6, 8, 10, 20, and 5 m above the deepest point of both basins.

over the deepest area of each lake basin. In each sampling series, floating nets were used at least one night in each depth zone (Fig. 3). These nets catch charr with body lengths 18–45 cm with approximately equal efficiency. In addition, young charr with body lengths 9–13 cm were caught with bottom nets (mesh size 10 mm) placed in chains from the

TABLE 2. Number of charr (*Salvelinus alpinus*) caught in Vangsvatnet Lake during May 1977–June 1979. Monthly number of individuals impossible to age is given in parentheses.

		Bottom nets		Floating nets		Nets and seine,	Other	
Year	Month	Upper basin	Lower basin	Upper basin	Lower basin	Saganeset	methods	Total
1977	May	71	39	—	44	—	40	194 (1)
	June	166	10	275	23	—	52	526 (6)
	July	103	35	172	19	—	8	337
	Aug.	93	18	254	198	—	2	565 (3)
	Sept.	54	34	186	165	—	3	442 (3)
	Oct.	47	128	170	88	89	3	525 (3)
	Nov.	58	137	59	156	253	9	672 (3)
	Dec.	51	92	77	135	65	26	446 (1)
1978	Jan./Feb.	59	—	44	53	17	9	182 (2)
	March	—	—	—	—	—	15	15
	April	50	167	128	90	—	5	440 (1)
1979	June	—	—	—	—	15	—	15
Total		752	660	1365	971	439	172	4359 (23)

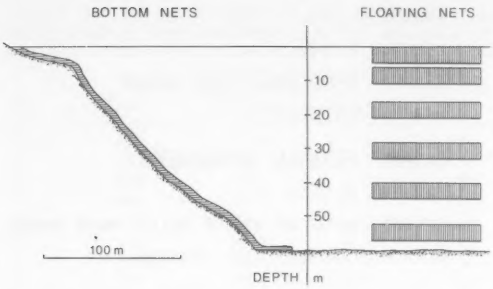

FIG. 3. Bottom and floating net representation in the upper basin of Vangsvatnet Lake during each sampling period.

shoreline to a depth of 50 m in the upper and 22 m in the lower basin. The distribution and food of these small charr have been treated separately from larger charr. During June–August 1979 we used a push-net (frame size 1.20 m × 0.40 m, mesh size 5 mm) in the spawning area at Saganeset (Fig. 1).

The charr caught were separated in the field according to their coloration into parr, dwarf charr, and normal charr. Further examination of the charr was carried out as soon as possible on the day of capture. We measured the natural tip length (Ricker 1979) to the nearest 0.1 cm and determined the sex and degree of sexual maturity according to Dahl (1917). The charr could be separated into sexually immature and mature individuals during October–March.

We were able to age 4336 (99.5%) of the charr by use of otoliths as described by Jonsson (1976). The alevins emerged in June. From emergence until June 1 the next year, the parr are classified as age-group 0. From this date to June 1 the year thereafter, they are classified as age-group 1, etc.

Stomach contents from 1653 charr (38%) were identified and counted under a stereoscopic microscope. Crustaceans were identified to species, mollusks to genera, chironomids to tribes, and other aquatic insects to orders. The average individual wet weight for each of the food categories was determined by weighing undigested food items from charr stomachs in each sampling series. All food items were dried for 1 min on ink paper and weighed to the nearest 0.05 mg. We calculated the weight percentage of each food item for every stomach, and the figures obtained were summed and divided by the number of stomachs investigated in each sampling series. This method expresses the average dietary state of the population during a certain time or at a certain place (Nilsson 1955). We based the calculations on reconstructed wet weights by counting partly digested food items as intact specimens.

All statistical tests in the present paper are based on a 5% significance level.

Results

DESCRIPTION OF CHARR MORPHS

The charr population of Vangsvatnet appears in two morphs (Fig. 4). One phenotype is pale brown with parr marks along the flanks and poorly developed spawning coloration. These fish are denoted parr in nonbreeding conditions and dwarf charr during the breeding season. The other phenotype is silvery with a pink sheen in nonbreeding conditions, and has bright red spawning colors. These are denoted normal charr. The young of both morphs have the same pale appearance (parr). In normal charr the shift in phenotype occurs at a body length of 15–27 cm.

The two morphs had an equal number of gill rakers at corresponding body lengths. Within the length interval 15–24 cm, where both morphs were represented, the average number of gill rakers was 25.2 for dwarf charr and 25.5 for normal charr (not significantly different according to Student's t-test: $t = 0.89$, df = 64, $P \approx 0.4$). The increase in number of gill rakers (y) with increasing body length (L, cm) can be approximated by the equation

$$(1) \quad y = 0.15\,L + 22.3 \qquad r = 0.50$$

for charr larger than 5 cm. Alevins 2–3 cm in length had only 4–8 gill rakers.

The flesh color of immature charr depended on both body length and morph. Among charr with body lengths 15–19 cm, white flesh was common in both morphs (~90%). At body lengths of 20–24 cm, 75% of the normal charr had pink or red flesh color, while 60% of the parr and dwarf charr still had white flesh. This difference in flesh coloration was highly significant (χ^2-test: $\chi^2 = 37.23$, df = 2, $P < 0.001$).

Maturing normal charr caught in September resembled immatures both in external (pink belly) and internal coloration (pink or red flesh). As the spawning time approached, the external coloration changed from pink to orange belly in most females and red in most males (Fig. 4). At the same time the intensity of the flesh color decreased from red and pink to white in mature normal charr. Among normal charr spawners 75% of the females and almost 100% of the males had white flesh. In maturing dwarf charr there was no conspicuous change either in belly color or flesh color during the autumn.

The first individuals to transform from parr to immature normal charr were 1 yr old (Table 3). These were among the largest individuals in the age-group (Jonsson and Hindar 1982). The frequency of normal charr increased in age-groups 2 and 3 for both sexes. From age-group 4 onwards, the frequency of normal charr among females was near 80%, among males the frequency increased to 100% in age-group 7. From age-group 4 on, there was a surplus of females among parr and dwarf charr, and of males among normal charr.

The coloration of the two morphs indicates that they occupy different habitats during the growth season. Parr and dwarf charr have a benthic daylight camouflage color (Noakes 1980), while normal charr have a pelagic daylight camouflage (Nikolsky 1963, p. 53). The two morphs also show differences in mouth position, the upper jaw being more overshot in parr and dwarfs than in normal charr (Fig. 4). This indicates an adaptation to benthic feeding for the parr and dwarfs (Nikolsky 1963, p. 270). On the other hand, both mouth position and the higher frequency of red flesh color indicate that zooplankton forms an important part of the food for normal charr.

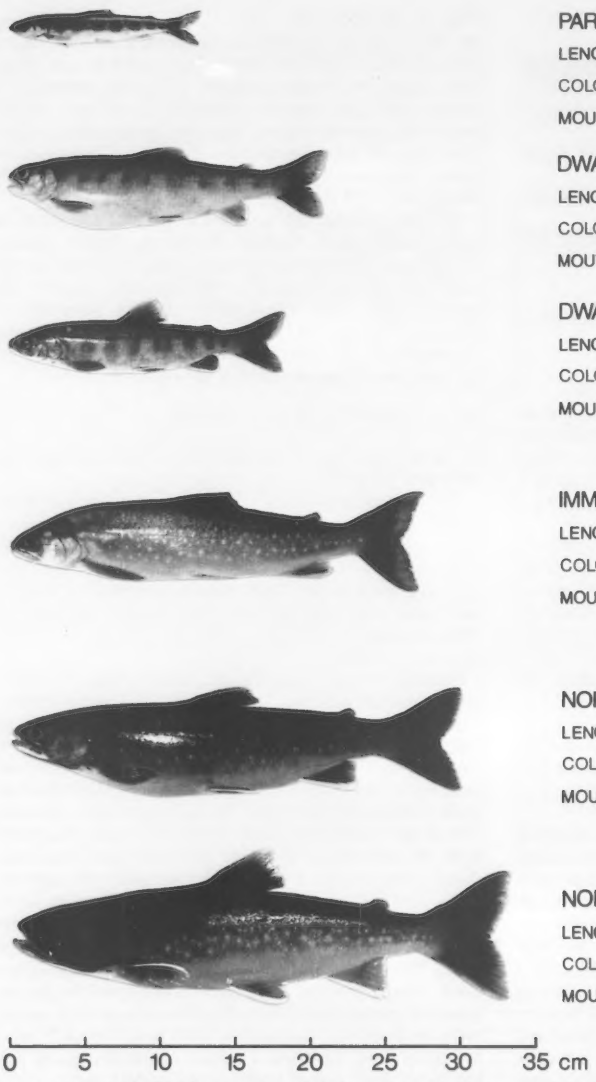
PARR
LENGTH: 2-25 cm
COLOR: WHITE BELLY, PARR MARKS
MOUTH: OVERSHOT
DWARF FEMALE SPAWNERS
LENGTH: 17-27 cm
COLOR: BEIGE OR WHITE BELLY, PARR MARKS
MOUTH: OVERSHOT OR TERMINAL
DWARF MALE SPAWNERS
LENGTH: 14-25 cm
COLOR: YELLOW OR BEIGE BELLY, PARR MARKS
MOUTH: OVERSHOT OR TERMINAL
IMMATURE NORMAL CHARR
LENGTH: 15-34 cm
COLOR: PINK OR WHITE BELLY, SILVERY SIDES
MOUTH: OVERSHOT
NORMAL FEMALE SPAWNERS
LENGTH: 20-36 cm
COLOR: ORANGE, RED OR PINK BELLY
MOUTH: OVERSHOT, TERMINAL OR UNDERSHOT
NORMAL MALE SPAWNERS
LENGTH: 18-43 cm
COLOR: RED OR ORANGE BELLY
MOUTH: UNDERSHOT, TERMINAL OR OVERSHOT
0 5 10 15 20 25 30 35 cm

FIG. 4. Stages in the life history of charr (*Salvelinus alpinus*) in Vangsvatnet Lake. The changes in phenotype from parr to normal charr, and from immature to mature individuals, are gradual, and intermediate forms are found (photos, T. A. Schei).

DISTRIBUTION

The bottom net catches of the two basins appeared to vary inversely during the sampling period (Fig. 5). In the upper basin the catches increased from May to a maximum in June, and then decreased to a low level from September to April. In the lower basin the catches decreased from May to a minimum in June–July, and then increased until next April. The floating net catches were also much higher in the upper than in the lower basin during June–July. From the autumn onwards, the floating net catches of the two basins were of more equal size.

In benthic areas the catches were generally distributed from a 5-m depth down to the greatest depths of both basins (Fig. 6). In shallow areas the distribution of charr was probably restricted by competition with brown trout, which dominated all littoral catches (0–5 m) numerically. In the pelagic zone of both basins the catches of charr were highest in the 0- to 5-m-depth interval during summer, and at 5–20 m or deeper during the rest of the year. Trout was abundant in near-surface waters during summer and autumn, and was

TABLE 3. Age and sex distribution of charr morphs (*Salvelinus alpinus*) caught in Vangsvatnet between June 1977 and April 1978.

Age	Total	Proportion normal charr (%)		Sex ratio, M/F
		Females	Males	
1	130	1.9	6.6	1.41
2	431	38.4	43.1	1.33
3	674	73.3	71.8	1.04
4	1486	80.3	83.2	1.05
5	1029	76.2	87.2	1.04
6	317	79.9	90.2	1.37
7	46	84.0	100.0	0.84
8	12	100.0	100.0	2.00
9	2	50.0	—	0.00
10	1	100.0	—	0.00
Total	4128	72.0	75.9	1.10

more restricted to the upper 1−2 m than the charr.

In the upper basin there was a marked habitat segregation between the two morphs during June−September (Fig. 6). Most parr and dwarfs were caught with bottom nets and with floating nets deeper than 40 m. Normal charr were at the same time mainly caught in the upper 20 m of the pelagic zone (i.e. limnetic). Some were also caught with bottom nets, usually in more shallow waters than parr and dwarf charr. These differences in distribution of the two morphs were highly significant; the frequency of normal charr being much higher in the limnetic zone than in benthic or deep-pelagic catches (χ^2-tests of June−September samples; limnetic versus benthic: $\chi^2 = 373.85$, df = 1, $P < 0.001$, limnetic versus deep-pelagic: $\chi^2 = 366.22$, df = 1, $P < 0.001$).

During the rest of the year there was no such habitat segregation between the two morphs in the upper basin. In October−November both morphs were found together in the upper 20 m of the pelagic zone and in the benthic zone. In December−January/February all catches were dominated by immature normal charr. At this time the catches of parr and dwarf charr and spent normal charr were generally low. Additional bottom net fishing near the river inlet (Fig. 1) also resulted in high catches of immature normal charr. In April−May both morphs were found both in benthic areas and in the pelagic zone. A significant trend of parr and dwarf charr to be caught deeper than normal charr persisted throughout the year in the upper basin, except for winter (Table 4).

In the lower basin the catches of parr and dwarf charr were small, and made up a significantly lower proportion of the catches than in the upper basin (χ^2-tests of May−April samples; bottom nets: $\chi^2 = 150.48$, df = 1, $P < 0.001$, floating nets: $\chi^2 = 74.34$, df = 1, $P < 0.001$). The habitat segregation of the two morphs was less conspicuous than in the upper basin, and there was no significant trend of parr and dwarf charr being caught deeper than normal charr. In October−November the bottom net catches in the lower basin consisted to a large extent of mature normal charr, indicating that this sampling locality lies on or near a spawning area.

The differences in distribution between the two morphs are reflected also in the variation of mean fish length with depth (Fig. 7). In the upper basin during June−September, both bottom nets and floating nets at 28−60 m caught charr with mean body lengths 18−22 cm. At the same time floating nets

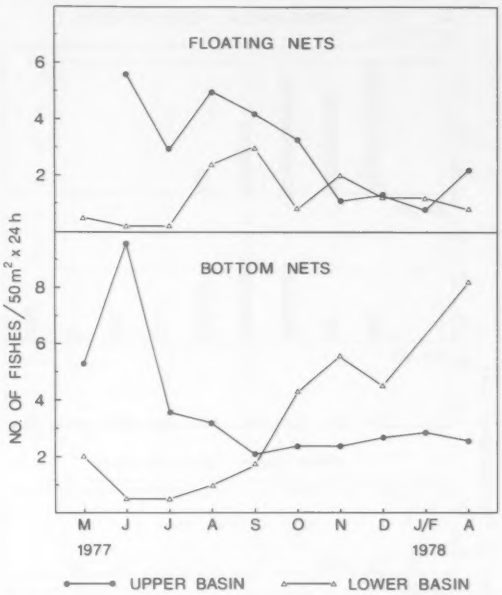

FIG. 5. Catch per unit effort of charr (*Salvelinus alpinus*) morphs caught with bottom and floating nets in the two basins of Vangsvatnet Lake during May 1977−April 1978.

in the upper 20 m caught significantly larger charr (mean length 26 cm; normal distribution test of limnetic versus benthic sample means: $d = 30.23$, 1090 df, $P < 0.001$, limnetic versus deep-pelagic sample means: $d = 23.09$, 1005 df, $P < 0.001$). Such differences in mean fish lengths were not found in the other catches (Fig. 7).

Age-groups 4 and 5 dominated most catches of charr in Vangsvatnet (Table 3). Younger age-groups were better represented in autumn and winter than in summer. In the upper 20 m of the pelagic zone the mean ages decreased from 3.8−4.7 yr in June−August to 3.2−4.0 yr in September−November. This is not merely a growth effect, as it occurred parallel to a decrease in the minimum size of limnetic charr from 18−21 cm to 15−17 cm.

Small parr (9−13 cm) were caught with bottom nets (mesh size 10 mm) during June 1977−April 1978. In April floating nets with mesh size of 10 mm were also used in an attempt to catch small parr in the pelagic zone, but these nets did not catch parr in either basin until they hung near the bottom.

The catch per unit effort of small parr was 3−10 times higher than for larger charr in June−October, but smaller in November−April. The largest catches of small parr were found deeper than 15 m in both basins throughout the sampling period. The age of these parr was 2 yr in summer catches and 1 yr during autumn, winter, and spring. This is probably a result of their growth. Among small parr a surplus of males was caught in all sampling periods in both basins.

FEEDING

The food of charr caught in the upper basin is given

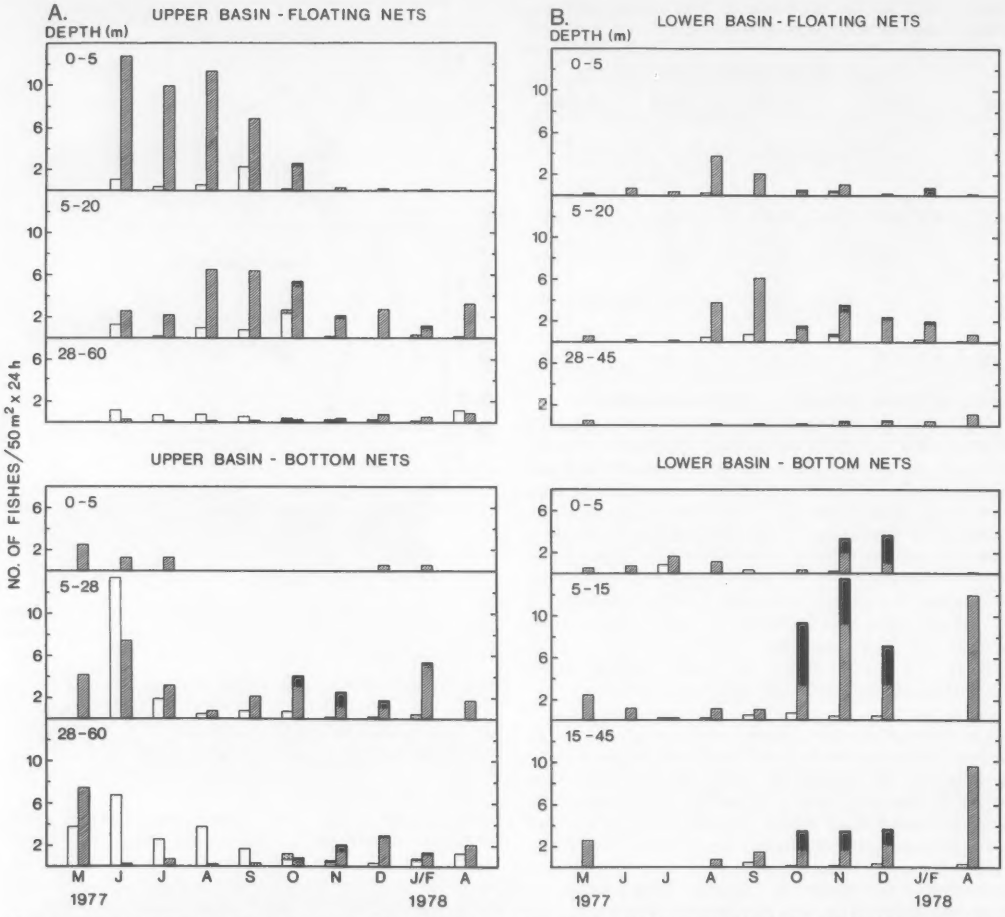

FIG. 6. Vertical distribution in the catch per unit effort of charr (*Salvelinus alpinus*) morphs caught with bottom and floating nets in the two basins of Vangsvatnet Lake during May 1977–April 1978. May–September and April: □, parr and dwarf charr; ▨, normal charr, October–January/February; □, parr, ▨, dwarf charr; ▨, immature normal charr; ■, mature normal charr.

in Fig. 8.

Zooplankton was a dominant food item for all normal charr, and for parr and dwarf charr caught in the pelagic zone at a 0- to 20-m depth, during the period July–November. Zooplankton was never important for parr and dwarf charr taken deeper than 28 m, either sampled with bottom or floating nets.

In June–July, *Bosmina longispina* was eaten by both charr morphs. *Cyclops abyssorum* was also eaten, but to a smaller extent, and never by individuals feeding on *B. longispina*. In August, both *Daphnia longispina* and *B. longispina* were main food items for charr, and *Bythotrephes longimanus* was also eaten by normal charr. These cladocerans often occurred together in the charr stomachs. In addition, some charr had also eaten *Holopedium gibberum*. In September–October, *D. longispina* was the dominating food item. In November, *B. longispina* was the important food for normal charr caught in the pelagic zone down to a 20-m depth.

Chironomid pupae were the dominating food item for most charr in June, and were also important in July. During these 2 mo, some charr also fed on adult chironomids at the surface. During the rest of the year, surface insects were unimportant food objects. In July, both charr morphs caught with bottom nets down to 28 m ate Trichoptera pupae.

Zoobenthos was the dominating food category during the period December–May for all charr. During the rest of the year, zoobenthos was also the most important food for parr and dwarf charr caught deeper than 28 m both with bottom and floating nets. Throughout the period, chironomid larvae of the tribe Chironomini made up the most important zoo-

TABLE 4. Test of significance (χ^2-tests) of the differences in vertical distribution of charr morphs (*Salvelinus alpinus*) in the upper basin of Vangsvatnet Lake during May 1977–April 1978 (cf. Fig. 6). (ns = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.)

	Parr and dwarf charr versus normal charr			
Method	Month	df	χ^2	Significance
Bottom nets	May	2	12.78	**
	June	2	17.04	***
	July	2	10.86	**
	Aug.	1	8.35	**
	Sept.	1	11.29	***
	Oct.	1	9.06	**
	Nov.	1	0.32	ns
	Dec.	2	2.84	ns
	Jan./Feb.	2	4.69	ns
	April	1	2.84	ns
Floating nets	June	2	172.96	***
	July	2	99.36	***
	Aug.	2	83.41	***
	Sept.	2	57.84	***
	Oct.	2	15.49	***
	Nov.	2	14.45	***
	Dec.	2	8.97	*
	Jan./Feb.	2	2.37	ns
	April	1	38.23	***

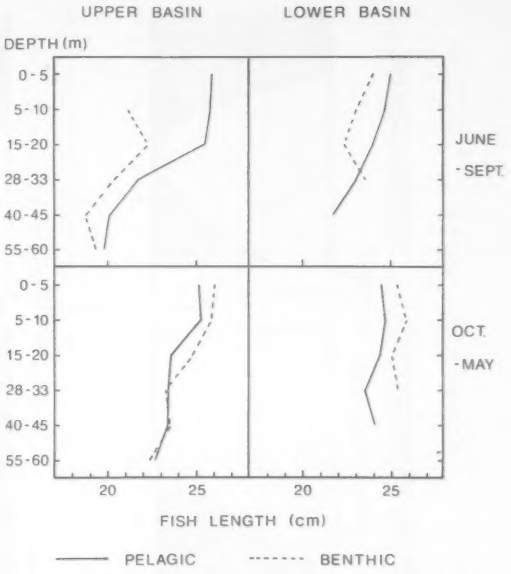

FIG. 7. Mean lengths of charr (*Salvelinus alpinus*) at various depth categories of the pelagic and benthic catches in the two basins of Vangsvatnet Lake during the periods June–September 1977 and October 1977–April 1978 (May 1977 included).

benthic food. Charr caught with bottom nets also fed on other chironomid larvae and *Pisidium* spp. throughout the year, and on the benthic copepod *Megacyclops gigas* during winter. Other benthic invertebrates occurred only sporadically in the charr stomachs. These were larvae of Plecoptera, Simulidae, Ephemeroptera, Trichoptera, Megaloptera; and Ostracoda, Nematoda, Oligochaeta, water beetles, water mites, and *Eurycercus lamellatus*.

Charr eggs occurred in some stomachs in December. Egg predation was further studied in November–December 1977 in the spawning area at Saganeset. Eggs were more frequently found in stomachs of spent charr than in ripe prespawning individuals. Immature individuals caught in the spawning area were also feeding on eggs. Eggs of trout were found in one charr stomach in both October and November, and eggs of threespine stickleback were found in one charr stomach in June.

Threespine stickleback were found in the stomachs of a few large charr only, and none of the charr caught preyed on other fish species. The low frequency of predatory charr in Vangsvatnet may be connected with the infestation of *Diphyllobothrium dendriticum* in stickleback. All predatory charr carried a large number of *Diphyllobothrium* cysts, which may decrease their fitness (Vik 1957).

Charr feeding on zooplankton had both the highest average weight of the stomach contents and the lowest frequency of empty stomachs in September–October (Fig. 9). Normal charr feeding on zoobenthos had the highest average weight of the stomach contents during April–May, when the frequency of empty stomachs was low. In winter, this tendency of an inverse relationship between the average weight of the stomach contents and the frequency of empty stomachs was not so consistent in normal charr. Parr and dwarf charr feeding on zoobenthos had the highest average weight of the stomach contents in December, when the frequency of empty stomachs was low. In September–October a low average weight of the stomach contents could coincide with a high frequency of empty stomachs.

The food of charr caught in the lower basin is given in Fig. 10 and 11. There the food of the charr differed in some aspects from the results found in the upper basin:

1) Zooplankton was the dominant food for both charr morphs during June–November. *Cyclops abyssorum* was more important during early summer and *B. longispina* during November and January/February compared with the upper basin. In addition, *D. longispina* was important in November.

2) Zoobenthos was less important than in the upper basin. Within the zoobenthos, *Pisidium* spp. and chironomid larvae other than Chironomini were also important.

3) The average weight of the stomach contents was lower than in the upper basin during winter and spring, when charr fed on zoobenthos. For normal charr the differences were significant, tested by Mann Whitney U-test (Elliott 1971, p. 112). In the lower basin, the highest average weight of the stomach contents was found in September–October, when charr fed on *D. longispina*. In this period the weight of the stomach contents of charr caught in the two basins was equal.

4) The frequency of empty stomachs was higher in the lower basin during winter and spring. The differences from the upper basin were significant for immature normal charr in December–January/February and for all normal charr in April–May (χ^2-tests).

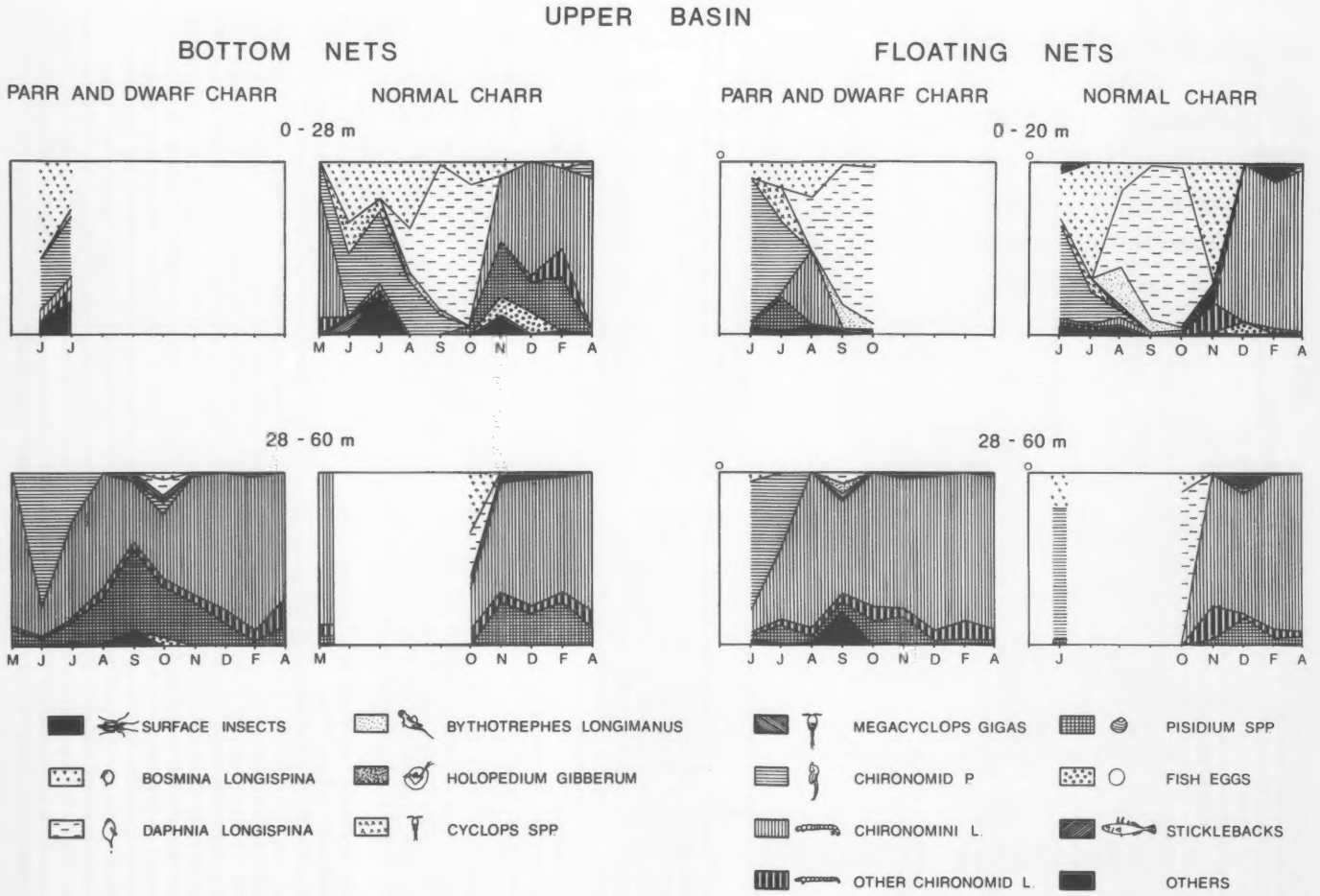

FIG. 8. Weight percentage composition of various food items in the stomach contents of charr (*Salvelinus alpinus*) caught with bottom and floating nets in the upper basin of Vangsvatnet Lake during May 1977–April 1978. Open areas indicate monthly catches of less than five fish, except for May 1977 when floating nets were not used (indicated by a dot).

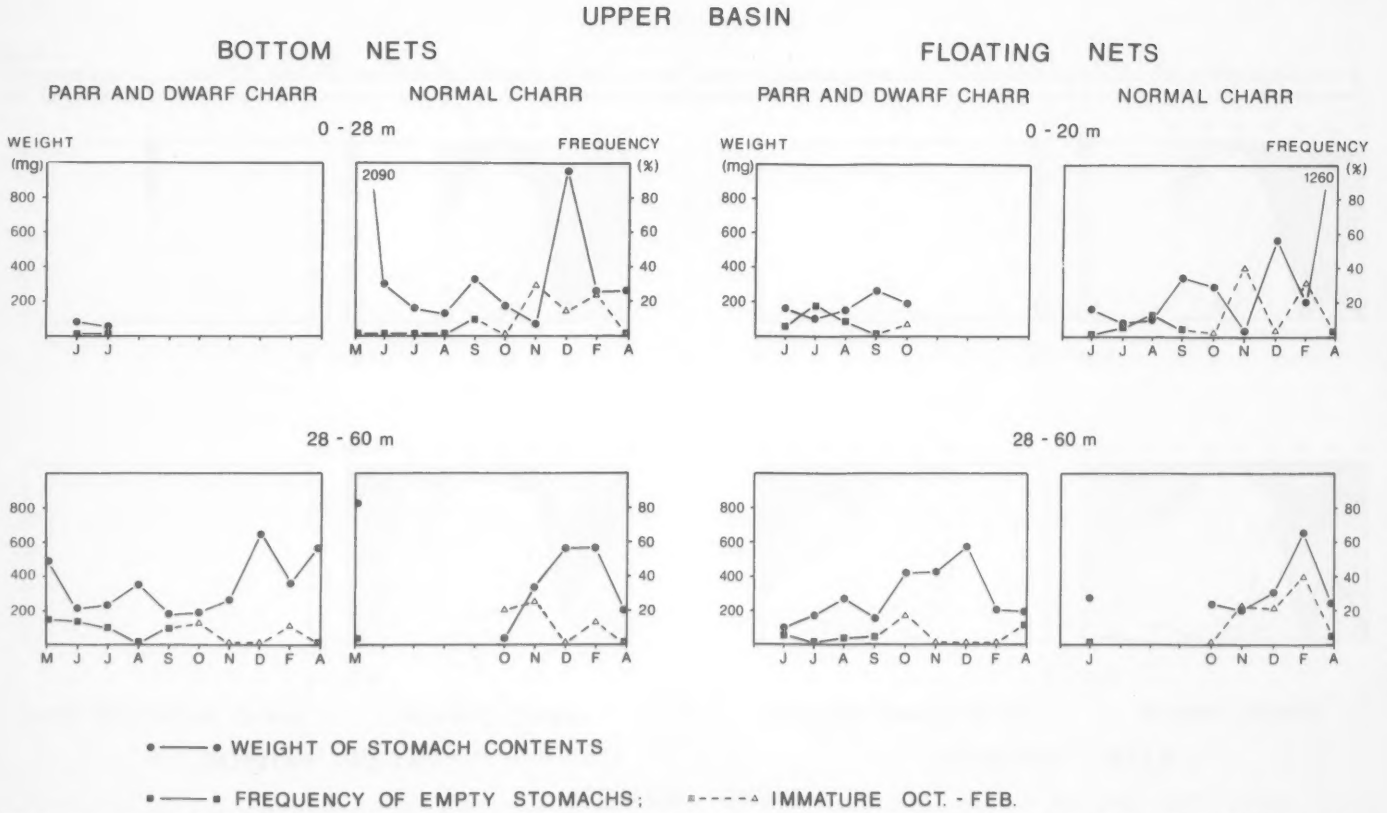

FIG. 9. Average weight of the stomach contents and frequency of empty stomachs in charr (*Salvelinus alpinus*) caught with bottom and floating nets in the upper basin of Vangsvatnet Lake during May 1977–April 1978 (cf. Fig. 8). The frequency of empty stomachs is given for immature charr during October–January/February.

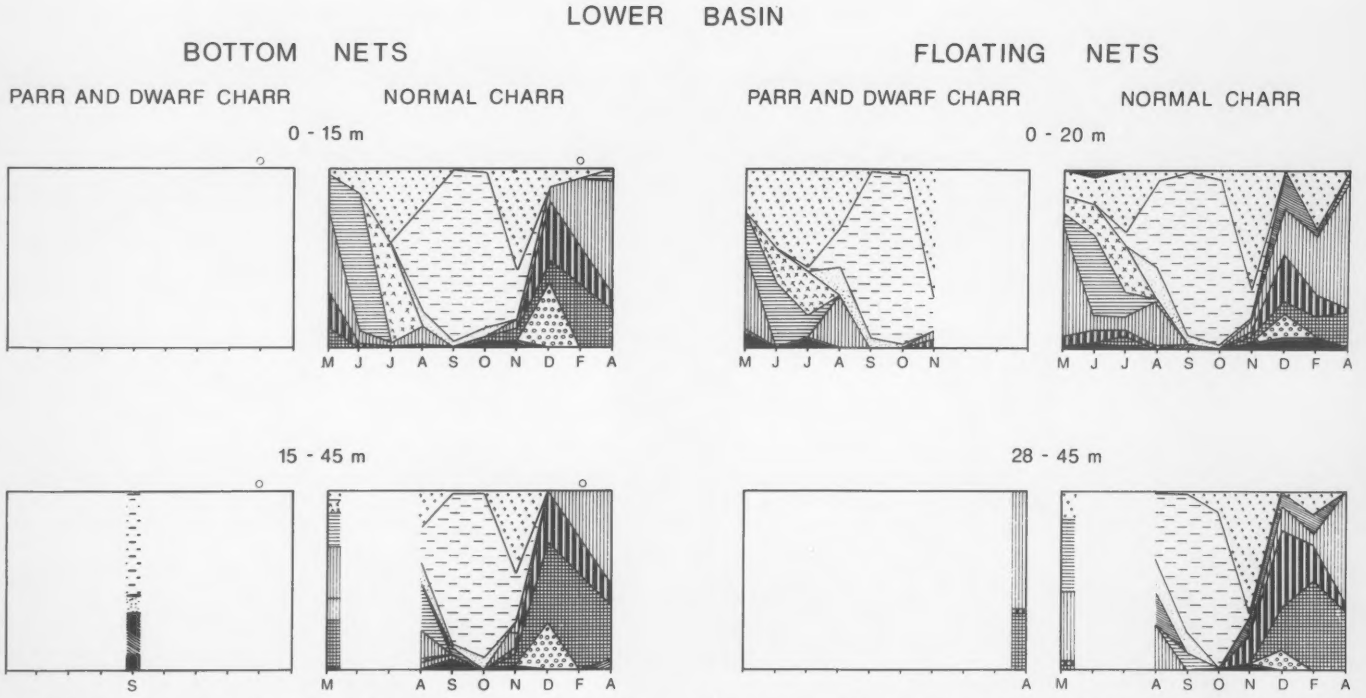
LOWER BASIN
BOTTOM NETS
FLOATING NETS
PARR AND DWARF CHARR
NORMAL CHARR
PARR AND DWARF CHARR
NORMAL CHARR
0 - 15 m
0 - 20 m
15 - 45 m
28 - 45 m
M J J A S O N D F A
M J J A S O N
M J J A S O N D F A
S
M A S O N D F A
A
M A S O N D F A

FIG. 10. Weight percentage composition of various food items in the stomach contents of charr (*Salvelinus alpinus*) caught with bottom and floating nets in the lower basin of Vangsvatnet Lake during May 1977–April 1978. Open areas indicate monthly catches of less than five fish. In January/February bottom nets were not used (indicated by a dot). Legend of food items as in Fig. 8.

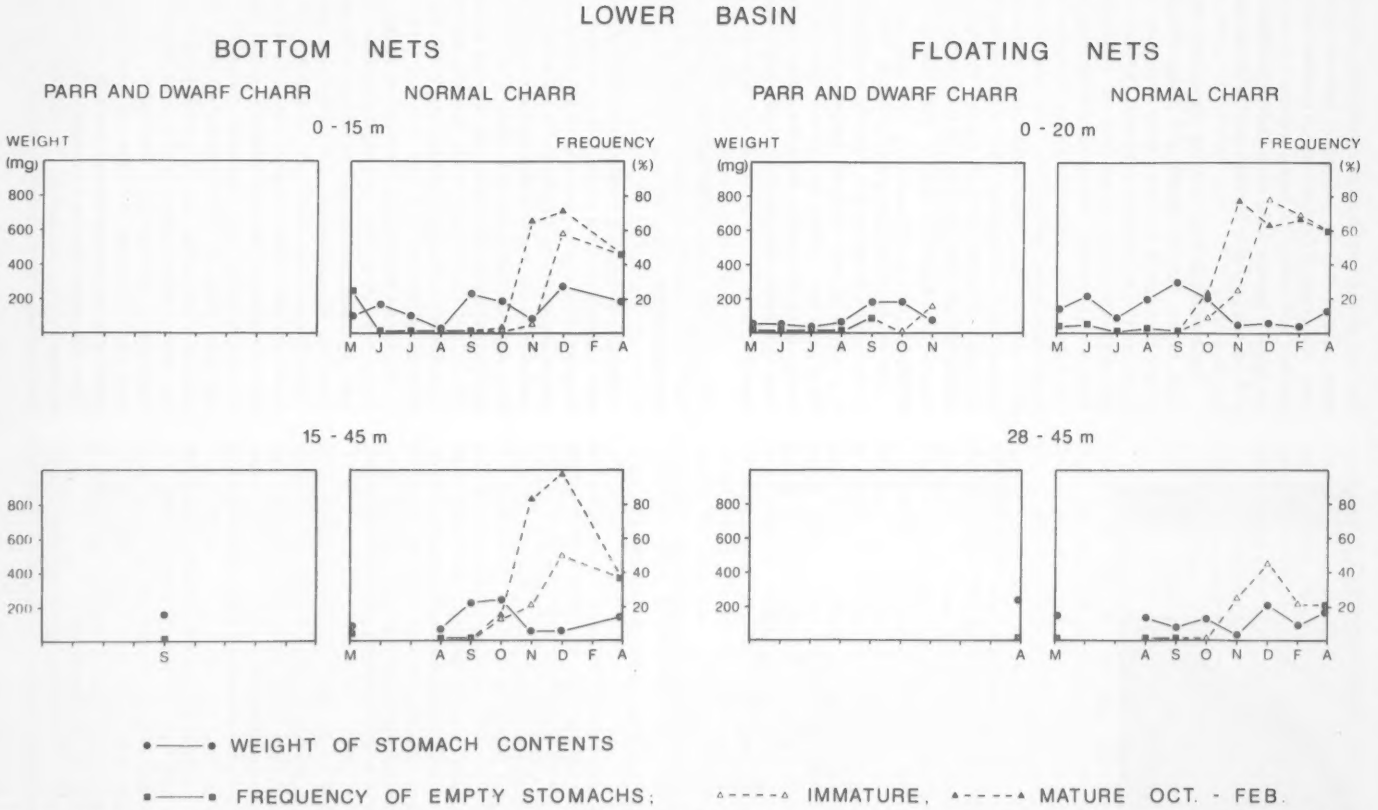

FIG. 11. Average weight of stomach contents and frequency of empty stomachs in charr (*Salvelinus alpinus*) caught with bottom and floating nets in the lower basin of Vangsvatnet Lake during May 1977–April 1978 (cf. Fig. 10). The frequency of empty stomachs is given separately for immature and mature charr during October–January/February.

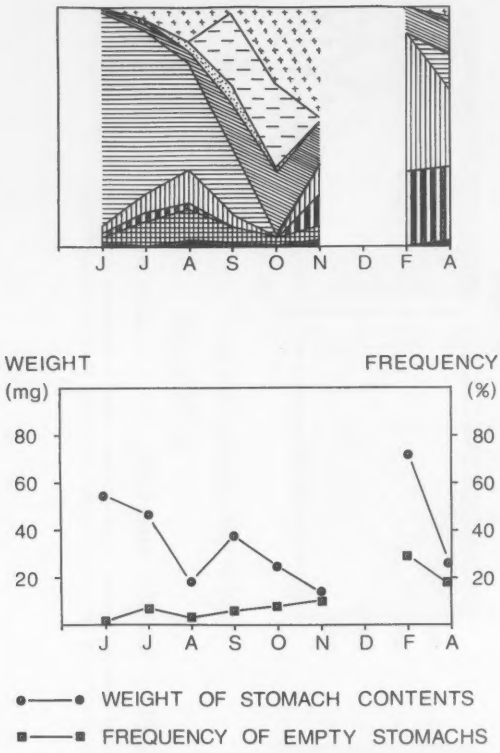

FIG. 12. Weight percentage composition of various food items, average weight of stomach contents, and frequency of empty stomachs in 9- to 13-cm-long parr (*Salvelinus alpinus*) caught with bottom nets in Vangsvatnet Lake during June 1977–April 1978. Open area in December 1977 indicates that less than five fish were examined. Legend of food items as in Fig. 8.

In the lower basin, sexually immature and mature charr could be compared with respect to the frequency of empty stomachs. Prior to spawning the frequency was higher for mature than for immature charr (November sample; $\chi^2 = 42.30$, df = 1, $P < 0.001$). From December on the frequency was the same.

Compared with larger charr caught with bottom nets, chironomid pupae and benthic copepods were more important food for small parr (Fig. 12). In April some of the small parr ate nauplii and young copepodids (I–III) of cyclopoid copepods. Larger charr never ate copepod stages other than adults and copepodids IV–V.

The average weight of the stomach contents of small parr was highest in June–July and January/February (Fig. 12). The small parr had eaten on average $\frac{1}{10}$th of the stomach contents of larger charr caught with bottom nets. The frequency of empty stomachs among small parr was highest in January/February, as with larger charr.

On June 19–20, 1979, 14 charr alevins with body lengths 2.1–2.7 cm were caught at a 17- to 34-m depth at Saganeset. The five alevins with stomach contents had all eaten one or more chironomid larvae, and four of them also benthic copepods. All but one of these alevins had resorbed their yolk sac, and they were among the largest specimens in the sample. In the smallest specimens the swim bladder was filled while the yolk sac was but feebly resorbed, and before any food objects had been taken.

Distribution and food analyses demonstrate that normal charr migrate between benthic and pelagic habitats, being pelagic from June to November when feeding on chironomid pupae and various zooplankton species. The catches also suggest that normal charr migrate from the lower to the upper basin in early summer, during the emergence period of the chironomids. From December to May, when the biomass of zooplankton is low, normal charr feed mainly on chironomid larvae in benthic areas. Normal charr never feed on littoral nor surface insects, except for May–June, during the peak emergence of aquatic insects. In contrast, trout fed heavily on surface insects throughout the ice-free period, and littoral insects were important food for trout during winter and spring.

Parr and dwarf charr live generally near the bottom, feeding on zoobenthos. In the autumn, when the zooplankton biomass is at its highest, some were also caught in the upper 20 m of the pelagic zone together with normal charr. In winter and spring, when both morphs are benthic, parr and dwarf charr were less active and generally caught deeper than normal charr.

Discussion

CHARR MORPHS

Immature individuals of charr were classified according to their camouflage dress, being either benthic or pelagic. Hitherto little has been known about the habitat and food of parr in deep lakes (Johnson 1980). Their coloration and mouth position (Fig. 4) suggested that they were mainly benthic in Vangsvatnet, feeding on zoobenthos. This was confirmed by the analyses of distribution and stomach contents. Individuals maturing sexually while in their parr stage were classified as dwarfs. Their distribution and food differed little from that of the parr.

The phenotypical change from parr to normal charr was accompanied by a change in habitat utilization. This shift in both phenotype and ecology corresponds to the smolt transformation in anadromous charr (Klemetsen and Grotnes 1980). Normal charr with bright red spawning colors developed from silvery-pink immature charr. The development of their nuptial dress occurred gradually during September–December, parallel with a reduction in flesh color from red and pink to white. It is known from fish rearing that individuals with a white flesh color do not develop as bright spawning colors as those with red or pink flesh (Mæland 1979). In Vangsvatnet, parr and dwarfs feeding on zoobenthos usually have white flesh color, while normal charr feeding on zooplankton in summer and autumn have pink or red flesh color. These differences may be the reason for the different spawning dress of the two morphs. The adaptive significance of the spawning coloration may be related to the reproductive

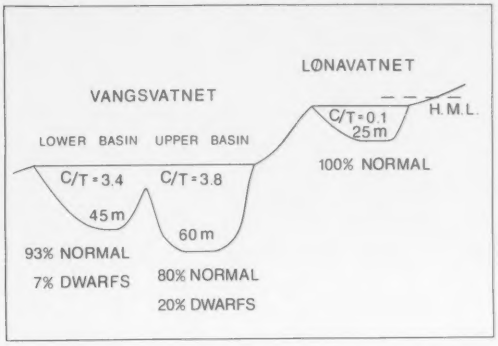

FIG. 13. Morph composition of charr (*Salvelinus alpinus*) in Vangsvatnet and Lønavatnet lakes in the Voss river system in relation to lake depth and charr to trout (C/T) ratio. H. M. L. represents highest marine limit during the postpleistocene inundation.

strategy of the charr, and is discussed by Jonsson and Hindar (1982).

HABITAT AND FOOD SEGREGATION

The habitat utilization of charr in Vangsvatnet appeared to be related to the size and coloration of the fish and may be explained by intraspecific competition between the two charr morphs and interspecific competition with the trout.

Because of their larger body size, normal charr are probably the stronger of the two morphs (cf. Wilson 1975). Their habitat utilization seems to be restricted by competition from trout. Trout dominated numerically the littoral catches except for May, during the most intensive emergence of littoral insects. In the pelagic zone, trout dominated the near-surface waters; surface insects made up a significant part of the trout's diet, but were only eaten by charr during the peak emergence of chironomids (June). As trout and charr show niche overlap only in periods when food is superabundant, the segregation of the two species in Vangsvatnet is probably interactive (Nilsson 1967).

In parallel, the two charr morphs show a marked segregation in habitat and food when food is scarce both in the benthic and pelagic habitat. This segregation is broken down in the autumn when zooplankton is abundant, and during winter and spring when the zoobenthos biomass is high. This dynamic picture shows that the spatial distribution of the two morphs is food dependent, and that the morph segregation is interactive. Thus we extend Nilsson's (1963, 1965) model to cover also the intraspecific competition between morphs. The competitive dominance of normal charr is probably related to an increased foraging efficiency with increasing body size. Charr may be aggressive toward one another, but they do not show territorial behavior when feeding (Noakes 1980).

The frequency of dwarf charr was higher in the upper than in the lower basin, and the habitat of dwarf and normal charr also was more segregated there. The upper basin is the deeper and probably holds a higher biomass of zoobenthos, especially chironomid larvae. Furthermore, 8 km upstream Vangsvatnet, in the trout-dominated and shallower Lønavatnet Lake, mature charr feature only one morph, normal charr (Fig. 13) (Jonsson and Østli 1979). Both Vangsvatnet and Lønavatnet Lakes are situated below the upper marine transgression line. In rearing experiments, Nordeng (1982) has shown that the development of charr progeny into two morphs in Vangsvatnet and one morph in Lønavatnet is heritable. This demonstrates that charr polymorphism is locally adapted, and thus we hypothesize that the occurrence of different charr morphs depends on the number of available niches during the growth season.

In simple fish communities, where charr live in allopatry or in sympatry with trout, as in many Scandinavian lakes, the charr may feature one or several phenotypes. In shallow lakes normal charr are found where both zoobenthos and zooplankton are abundant, often with the presence of predatory individuals where food fishes are available (Filipsson and Svärdson 1976). When zoobenthos is especially rich, normal charr may reach considerable size (Schmidt-Nielsen 1939). In alpine and arctic lakes where the zooplankton community is small or nonexistent, all charr may be dwarfs except for cannibalistic individuals (Klemetsen and Østbye 1967; Skreslet 1973). In deep lakes, charr often feature more than one morph, as in Vangsvatnet. These may consist of a benthic dwarf morph, a pelagic normal morph, and a predatory morph. In lakes where charr live in allopatry, normal charr may occupy the habitats used by trout in Vangsvatnet, while dwarf charr use both zooplankton and zoobenthos in deep areas (Nilsson 1955; Aass 1973). When charr is present in complex fish communities, it usually features only one morph. This may consist of dwarfs, normal charr, or predatory charr, depending on the available niches in the locality (Savvaitova 1973, 1980).

The occurrence of sympatric charr forms is by this hypothesis a locally adapted phenomenon. This is in accordance with the 'ecological polymorphism' of Savvaitova (1961, 1980). Behnke (1972, 1980) has suggested that charr forms may develop sympatrically to speciation. In Vangsvatnet, however, the two charr forms have to feed on both zooplankton and zoobenthos, which prohibits the food specialization needed for sympatric speciation (Maynard Smith 1966).

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NOTES

Thermal Habitat Shifts by Fishes at the Thermocline in Lake Michigan

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CROWDER, L. B., AND J. J. MAGNUSON. 1982. Thermal habitat shifts by fishes at the thermocline in Lake Michigan. Can. J. Fish. Aquat. Sci. 39: 1046–1050.

We documented thermal habitats of Lake Michigan fishes by bottom trawling at the intersection of the thermocline and the lake bottom near Grand Haven, Michigan. Fish distribution by temperature strata was surveyed during day and night on September 7–13, 1977, and repeated on August 27–September 1, 1979. In the interim, bloaters (*Coregonus hoyi*) had increased substantially. By comparing these two periods, we suggest that bloaters dramatically altered the thermal distribution of adult alewife (*Alosa pseudoharengus*). While comprising less than 1% of the trawl catch in 1977, bloaters comprised 42% in 1979. Bloaters were the most-abundant species from 5 to 16°C in 1979. Adult alewife shifted their thermal distribution from 11 to 16°C in 1977 to 4 to 8°C in 1979. This shift is interpreted in terms of competition for food and thermal habitat, or predation by salmonids. The idea that the altered thermal distribution of alewife results from competitive interactions with bloaters is favored by existing data.

Key words: competition, fishes, habitat partitioning, Lake Michigan, niche shift, predation, salmonids, temperature, thermocline

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Des chalutages sur le fond à l'intersection de la thermocline et du fond près de Grand Haven, au Michigan, nous ont permis de définir les habitats thermiques de poissons du lac Michigan. Nous avons déterminé leur répartition par couches thermiques, le jour et la nuit, du 7 au 13 septembre 1977 et de nouveau du 27 août au 1er septembre 1979. Dans l'intervalle, le cisco de fumage (*Coregonus hoyi*) avait augmenté de façon appréciable. Après avoir comparé ces deux périodes, nous suggérons que le cisco de fumage a modifié dramatiquement la distribution thermique du gaspareau (*Alosa pseudoharengus*) adulte. En 1977, le cisco de fumage représentait moins de 1% des prises du chalut, tandis qu'en 1979 ce pourcentage était passé à 42. En 1979, le cisco de fumage était l'espèce la plus abondante entre 5 et 16°C. Le gaspareau adulte a modifié sa distribution par rapport à la température, de 11 à 16°C en 1977 à 4 à 8°C en 1979. Nous interprétons ce glissement en termes de compétition pour la nourriture et l'habitat thermique, ou de prédation par les salmonidés. Les données actuelles appuient l'hypothèse que le changement de distribution du gaspareau résulte d'interactions compétitives avec le cisco de fumage.

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FISH and other taxa shift niches in response to the presence of competitors (Nilsson 1967; Colwell and Fuentes 1975; Werner and Hall 1976, 1979; Sale 1979), and these shifts have been considered evidence for contemporary competition (Schoener 1974; Diamond 1978). Field experiments involving direct manipulations of interspecific competition in fishes are relatively rare (Werner and Hall 1976, 1979) and may be impractical, particularly in large systems (such as Lake Michigan) where both competition and predation are potentially important mechanisms (cf. Connell 1975, 1980).

Temperature is an important niche dimension to fishes (Fry 1971; MacLean and Magnuson 1977; Magnuson et al. 1979) as well as to terrestrial ectotherms (Huey and Slatkin 1976). Even small changes in temperature can have important bioenergetic consequences to an organism's survival, growth, or reproductive success (Kitchell et al. 1977; Crowder and Magnuson 1982). Common Lake Michigan fishes segregate based on habitat temperature (Brandt et al. 1980), and their diets are complementary to thermal habitat use (Crowder et al. 1981). In this paper, we present observational evidence of a thermal niche shift by alewife (*Alosa pseudoharengus*) in Lake Mich-

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igan. This shift follows a dramatic increase in the abundance of a native cisco, the bloater (*Coregonus hoyi*). The observed shift may be due to competition with bloater, though predation and other mechanisms cannot be ruled out.

Methods — The intersection of the thermocline with the bottom provides an opportunity to examine habitat use along a rather sharp and dynamic thermal gradient (Emery 1970; Mortimer 1971; Brandt et al. 1980). We measured the distribution of fishes where the thermocline intersected the bottom near Grand Haven, Michigan. Samples were taken day and night by bottom trawling along bottom isotherms from September 7–13, 1977 and August 27–September 1, 1979 (cf. Brandt et al. 1980).

Fish were counted, identified, and all individuals of a species up to 50 per trawl haul were preserved. At each station, vertical temperature profiles were determined with a 60-m bathythermograph (BT). In 1977, a thermister was attached to the headrope of the trawl to aim the trawl along isotherms. Generally, constant trawling temperatures were maintained by steering along depth contours (Brandt et al. 1980). Because of a thermister malfunction in 1979, trawl temperatures for each tow were estimated by the average of the bottom temperature at the beginning and end of each trawl towed along a depth contour. For 48 tows (27 day, 21 night) the average difference in beginning and end bottom temperature was only 0.6°C (range 0.4–4°C). Because several common species vertically migrate at night (Brandt et al. 1980), we will focus our analysis on day trawl catches.

To provide sufficient replication for each thermal stratum, we divided the trawl data into four thermal strata, each ~4°C wide, which correspond to the hypolimnion, lower metalimnion, upper metalimnion, and epilimnion. Strata following were established from examination of the temperature–depth profiles from each cruise (1977: 4.0–8.2, 8.3–12.2, 12.3–16.2, 16.3–19.5°C; 1979: 4.5–8.0, 8.1–11.5, 11.6–15.0, 15.1–18.7°C).

Geometric mean of catch per unit of effort (15 min bottom time) was calculated for each 2°C interval. Comparisons among catches for each species at different thermal strata were made using Kruskal–Wallis ANOVA (Hollander and Wolfe 1973) and Dunn's (1964) multiple comparison test ($\alpha = 0.1$).

Results — Composition of trawl catch — A total of 16 170 fish of 19 species were caught in 48 bottom trawls in 1979 (Table 1). Relative to 1977, the bloater increased from less than 1% of the catch to nearly 42% in 1979. Adult alewives also increased from 6 to 14% of the catch. Bloater, spottail shiner (*Notropis hudsonius*), rainbow smelt (*Osmerus mordax*), and alewife were the most abundant species in 1979 and accounted for 90% of the total catch as compared to 77% for these species in 1977. Because bloater sizes were distinctly bimodal small (80–145 mm fork length (FL)) and large (146–300 mm FL), we analyzed the thermal habitats of these groups separately. Small bloaters were probably yearlings based on their size (Edward Brown, Great Lakes Fishery Lab, U.S. Fish and Wildlife Service, Ann Arbor, MI), but we did not age individuals. Lengths of most other species were reasonably uniform and generally similar to 1977 (cf. Brandt et al. 1980). Alewives were slightly larger in 1979 (1977 mode 130 mm FL, 1979 mode 150 mm FL).

Differences among thermal strata — The distributions of each of the eight most-abundant species-size groups differed sig-

TABLE 1. Total catch of fish for day and night bottom trawls in 1979, listed in order of decreasing abundance. Percent total catch are included from 1977 (N = 20 352) for comparison (Brandt et al. 1980).

Species	Life stage	Numbers			% total	
		Day	Night	Total	1977	1979
Bloater	Small (80–145 mm)	4249	532	4781	0.3	29.6
	Large (146–300 mm)	1576	381	1957		12.1
	Total	5825	913	6738	0.3	41.7
Spottail Shiner		1855	897	2752	22.7	17.0
Rainbow Smelt	Adult	967	178	1145	6.3	7.1
	Young-of-the-year	1131	458	1589	10.0	9.8
	Total	2098	636	2734	16.3	16.9
Alewife	Adult	2174	120	2294	5.5	14.2
	Young-of-the-year	4	33	37	32.5	0.2
	Total	2178	153	2331	38.0	14.4
Slimy sculpin		49	591	640	1.0	4.0
Trout-perch		180	378	558	16.7	3.5
Ninespine stickleback		23	141	164	0.3	1.0
Yellow perch		80	60	140	2.1	0.9
Other species		39	74	113	0.7	0.6
	Total fish	12327	3843	16170	98.1	100.0
	No. trawls	27	21	48		

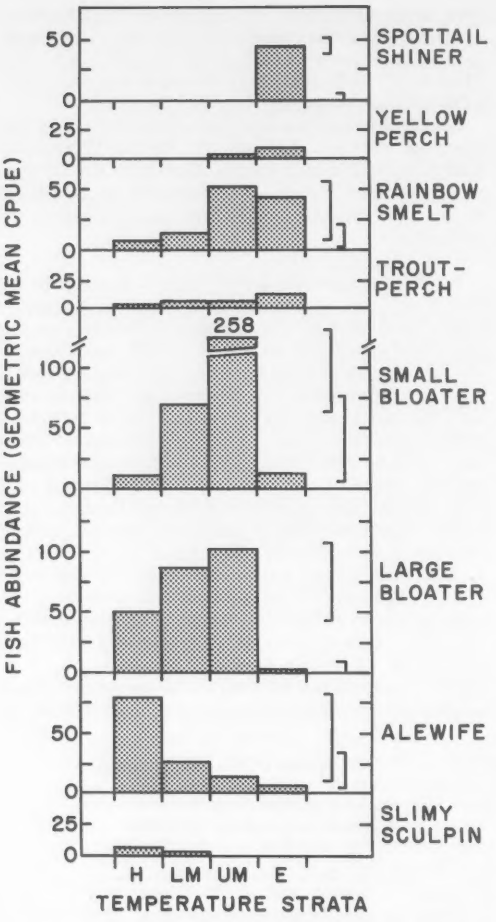

FIG. 1. Abundance of fish species with significant temperature distributions in 1979 (geometric mean catch per unit of effort (CPUE)) in Lake Michigan during day for each temperature strata (H, hypolimnion; LM, lower metalimnion; UM, upper metalimnion; E, epilimnion). Brackets indicate strata that did not differ (Dunn's test, $P < 0.1$). For yellow perch, significant differences were E > LM = H; for trout-perch, E > H; for slimy sculpin, H > E = UM.

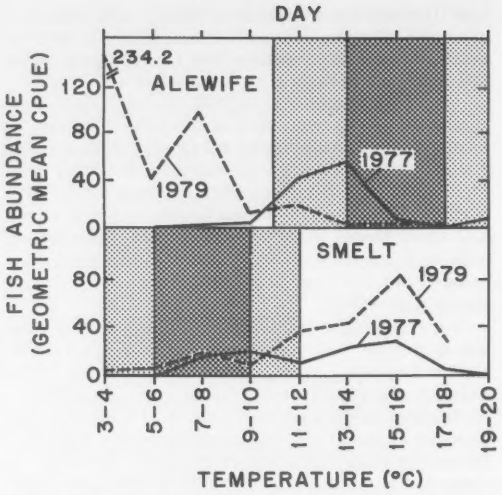

FIG. 2. Thermal habitat shift of adult alewife and rainbow smelt between 1977 and 1979. Fish abundance (geometric mean catch per unit of effort (CPUE)) is plotted vs. 2°C temperature strata. Shaded area overlays the expected thermal niche for each species (dark = preferred temperature ± 2°C, light = preferred temperature ± 5°C, cf. Magnuson et al. 1979).

nificantly with temperature (Kruskal–Wallis ANOVA: spottail shiner ($P < 0.025$), adult rainbow smelt (60–210 mm FL, $P < 0.01$), trout-perch (*Percopsis omiscomaycus*, $P < 0.025$), small bloater ($P < 0.01$), large bloater ($P < 0.01$), adult alewife (80–200 mm FL, $P < 0.01$), slimy sculpin (*Cottus cognatus*, $P < 0.01$), and yellow perch (*Perca flavescens*, $P < 0.005$)), during day when all species are common near bottom. Thermal habitat partitioning similar to that observed in 1977 (Brandt et al. 1980) was apparent (Fig. 1). Though too few young-of-the-year alewives were caught to show significant thermal distributions, they again shared the epilimnion (15–19°C) with spottail shiner, yellow perch, and trout-perch (cf. Brandt et al. 1980). Spottail shiner were significantly more abundant in the epilimnion than elsewhere (Dunn's test, $P < 0.1$, Fig. 1) as was generally true in 1977 (Brandt et al. 1980). Yellow perch and trout-perch distributions (Fig. 1) were similar to those in 1977 as well.

Rainbow smelt were significantly more abundant in the epilimnion and upper metalimnion than in the hypolimnion (Dunn's test, $P < 0.1$, Fig. 1). Their distribution was similar to 1977 also, except that in 1977, smelt were also more abundant in the lower metalimnion than in the hypolimnion (Dunn's test, $P < 0.1$).

Small bloaters were more common in the upper metalimnion than in either the epilimnion or hypolimnion (Dunn's test, $P < 0.1$, Fig. 1). Large bloaters occurred in the epilimnion less frequently than elsewhere along the thermal gradient (Dunn's test, $P < 0.1$, Fig. 1). Few bloaters were caught in 1977 (Brandt et al. 1980); those that were caught occupied the upper metalimnion and epilimnion.

Adult alewives were significantly more abundant in the hypolimnion than in the epilimnion (Dunn's test, $P < 0.1$, Fig. 1). This contrasts 1977 (Brandt et al. 1980), when alewives were more abundant in the upper metalimnion than in the hypolimnion (Dunn's test, $P < 0.1$).

Ninespine stickleback (*Pungitius pungitius*) and slimy sculpin were again caught primarily at cold temperatures (4–6°C). Significantly more slimy sculpins were caught in the hypolimnion than were caught in the epilimnion or upper metalimnion (Dunn's test, $P < 0.1$, Fig. 1).

1977 versus 1979 — The striking difference between 1977 and 1979 was the abundance of bloater, which was too rare to examine in 1977. In 1979, bloater was the most-abundant species in trawls from 5 to 16°C. Relative to 1977, adult

alewives shifted from temperatures near their laboratory preferred temperature (16°C, Otto et al. 1976) to cooler temperatures (Fig. 2). Alewives in 1977 were significantly more abundant in the upper metalimnion than in the hypolimnion, but in 1979 alewives were in cooler water. Significantly more alewives were caught in the hypolimnion in 1979 than were caught there in 1977 (Mann-Whitney U, $P < 0.001$). The alewife shift appears to have been sustained in 1980. Significantly more alewives were caught in the hypolimnion in 1980 than we caught there in 1977 (Mann-Whitney U, $P < 0.001$, Crowder and Magnuson unpublished data). In 1977, 93% of day-caught alewives occurred at their preferred temperature ±5°C, and 52% were caught within 2°C of their laboratory preferred temperature (Fig. 2, Magnuson et al. 1979). In 1979, only 8% of alewives were caught within 5°C of their preferred temperature and less than 3% occurred within 2°C of preferred temperature.

Rainbow smelt in 1979 occupied slightly warmer water than in 1977 (Fig. 2). In 1977 smelt were significantly more abundant in the lower metalimnion, upper metalimnion, and epilimnion than in the hypolimnion. In 1979 only the epilimnion and upper metalimnion were significantly higher. Data taken from 1977 to 1979 off Port Sheldon, Michigan, about 16 km south of our study site, tend to corroborate a thermal shift in rainbow smelt (Jude et al. 1980). In 1977–78, adult rainbow smelt were widely distributed within the metalimnion (6–14°C), but in 1979, they were caught most commonly at 10–16°C (Jude et al. 1980). These patterns agree with our data; rainbow smelt may also have shifted thermal habitat.

Discussion — The shift in thermal habitat of alewives was associated with an increase of bloater. Small bloaters were most abundant in the upper metalimnion in 1979 where adult alewives had predominated in 1977. In 1979, large bloaters were also most common in the metalimnion, though they were also abundant in the hypolimnion, overlapping the peak in alewife abundance. No thermal habitat shifts were apparent among the other native species between 1977 and 1979 although rainbow smelt may have shifted to slightly warmer water.

Exploitation competition between bloater and alewife may account for the observed shifts. Large bloaters overlapped with alewife in habitat, but their diets differed. Alewives, small bloaters, and rainbow smelt eat zooplankton (Crowder et al. 1981; Crowder unpublished data), and large bloaters (146–300 mm) eat primarily benthic prey (Wells and Beeton 1963; Crowder unpublished data). Small bloaters appear to have occupied the thermal habitat between rainbow smelt and alewife and so may have displaced alewife and rainbow smelt through competition for food. Other species did not shift their thermal distributions — they use different foods than alewife, bloater, and smelt (Crowder et al. 1981).

Cost benefit analysis of feeding behaviors of alewife and bloater in the laboratory indicate the two species do nearly equally well on large zooplankton and that alewives are probably more efficient feeding on small zooplankton (Janssen 1978; Crowder and Binkowski unpublished data). Bloaters also appear to be more efficient than alewife at taking prey near the bottom (Janssen 1978). Zooplankton within 1 m of the bottom in our trawling sites were relatively large (Crowder unpublished data). So bloaters may have had a foraging advantage relative to alewife feeding in the near-bottom habitat.

Interference competition cannot be eliminated as a factor in the observed niche shift. In laboratory aquaria, bloaters were behaviorally more aggressive than alewives and were more successful than alewives at capturing prey introduced to the surface (F. P. Binkowski, Great Lakes Research Facility, University of Wisconsin-Milwaukee, WI). Too little evidence exists to evaluate fully this hypothesis.

The alewife distribution may also have been altered by salmonid predation. Alewives are heavily preyed upon by salmonids in Lake Michigan (see Stewart et al. 1981 for a recent review). Lake trout eat predominantly alewives, though rainbow smelt and sculpins are also consumed (Rybicki and Keller 1978). Coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) eat alewives almost exclusively (D. Jude and T. Miller, Great Lakes Research Division, University of Michigan, Ann Arbor, MI). Yearling lake trout prefer water temperatures of 11.7°C (McCauley and Tait 1970), but older individuals often occupy ~10°C water (Ferguson 1958, Spangler and Berst 1976). Laboratory thermal preferences of coho and chinook are about 13°C (Brett 1962). If most of the predators occur between 10 and 13°C, then predation pressure is highest near the peak of the 1977 alewife distribution. To follow the 1979 alewife peak in distribution, the salmonid predators would have to move to waters 6–9°C cooler than preferred. While this predator shift is possible, it is probably infrequent (Coutant and Carroll 1980) and perhaps bioenergetically costly (Magnuson and Beitinger 1978; Crowder and Magnuson 1982). Because our total catch of alewife was not reduced in 1979 relative to 1977, and as predation intensity by salmonids did not change drastically between 1977 and 1979 (Stewart et al. 1981), the hypothesis that salmonid predation accounts for the observed habitat shift in alewife is not strongly supported.

The shift in alewife distribution might be explained by seasonal offshore migration. Alewives move offshore in late fall as the thermal stratification of the lake decays (Wells 1968). Our data indicate that in late August 1979, alewives were most abundant at depths of 40 m or greater. In 4 yr of data from the 1960s most alewives on comparable dates occupied a zone around 25 m (Reigle 1969). The mode of the alewife distribution did not approach 40 m until late November (Reigle 1969). In a similar survey in August 1980 (Crowder and Magnuson unpublished data), we again found alewives abundant in cold deep water relative to 1977. As we have shown (Brandt et al. 1980), depth distributions of fishes can be misleading if in fact they are responding more strongly to temperature or other variables. The possible shift in rainbow smelt toward warmer water is contrary to its seasonal habitat distribution (Wells 1968). Early seasonal offshore migration by alewife cannot be excluded as a hypothesis, but it seems unlikely.

Simple observational data on niche shifts cannot demonstrate conclusively that competition is the underlying mechanism (Connell 1975; MacLean and Magnuson 1977; Sale 1979). Competition is taken as the most frequent explanation for niche shifts (Diamond 1978). But predation and between-site or between-year variation may also explain the observed shifts in thermal habitat use (Connell 1975, 1980; Sale 1979).

The observed thermal habitat shift in alewife is statistically significant, and alewives were also more abundant in the hypolimnion in 1980 than they were in 1977 (Crowder and Magnuson unpublished data), so the shift may well have been sustained. The most plausible underlying mechanism for this observed habitat shift in alewife seems to be competition with small bloaters though predation by salmonids and other mechanisms cannot be ruled out. That alewife and perhaps rainbow smelt shifted and other species did not suggests competition, particularly as alewife and smelt diets are similar to that of small bloaters. We are continuing to examine these hypotheses in both the field and the laboratory.

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Macroinvertebrate Subsampling: A Simplified Apparatus and Approach

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WRONA, F. J., J. M. CULP, AND R. W. DAVIES. 1982. Macroinvertebrate subsampling: a simplified apparatus and approach. Can. J. Fish. Aquat. Sci. 39: 1051 – 1054.

A simple, inexpensive, volumetric, subsampling apparatus for processing macroinvertebrate samples is described. Random mixing of the macroinvertebrates was consistently achieved with the subsampler when applied to either lotic or lentic samples. Protocols for the use of the subsampler are forwarded for the situations when either reliable population density estimates or only general trends in community composition and abundance are required.

Key words: subsampling, macroinvertebrates

WRONA, F. J., J. M. CULP, AND R. W. DAVIES. 1982. Macroinvertebrate subsampling: a simplified apparatus and approach. Can. J. Fish. Aquat. Sci. 39: 1051 – 1054.

On trouvera dans l'article qui suit une description d'un appareil de sous-échantillonnage volumétrique, simple et peu dispendieux, servant à traiter des échantillons de macroinvertébrés. On obtient toujours un mélange aléatoire des macroinvertébrés, que l'appareil soit appliqué à des échantillons lotiques ou lentiques. Le sous-échantillonneur convient bien à des situations qui nécessitent soit des estimations fiables de densité de population, ou seulement des tendances générales de composition et d'abondance des communautés.

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THE large amount of labor required to process lotic and lentic macroinvertebrate samples has stimulated the development of numerous subsampling techniques (reviewed by Waters (1969) and Hickley (1975)). Optimally, subsampling should be performed with the minimum of effort while yielding the maximum amount of information. Additionally, the subsampler should be cheap to construct, easy to operate and maintain, and most important of all, should yield statistically reliable results.

Numerous subsampling procedures were tested in our laboratory, including those of Waters (1969) and Hickley (1975). Many inadequacies were found, including high construction costs, complexity in construction and operation, a restriction to the types of macroinvertebrate samples which could be subsampled, and a lack of mechanical and statistical reliability.

In this note we describe a simplified, inexpensive, volumetric subsampling apparatus that can be applied to a wide range of sample types, and suggest a protocol for its use.

Statistical methods — To estimate the total number of macroinvertebrates from subsample counts, it is necessary to establish that the macroinvertebrates are randomly distributed in the subsampler. This was accomplished by calculating the Index of Dispersion which is based on the variance to mean ratio of the subsample counts, and tests for conformity to a Poisson series. Because the index approximates a Chi-squared distribution, the following relationship was used:

$$(1)\quad I_{\mathrm{df}=(n-1)} = \chi^2_{\mathrm{df}=(n-1)} = \frac{S^2(n-1)}{\bar{x}} \quad \text{when } n < 31$$

where I = Index of Dispersion, χ^2 = Chi-squared statistic, n = number of subsampling units taken, S^2 = sample variance, $\bar{x}$ = sample mean, and $n - 1$ = degrees of freedom (Elliott 1977).

Agreement to a Poisson series was checked by examining whether the calculated χ^2 approximation value occurred between the 0.05 significance levels of the theoretical percentage points of the χ^2 distribution (Pearson and Hartley 1966).

Precision of the estimate (± 95% confidence limits) of the total number of individuals per taxon in the original sample was determined using the relationship:

$$(2)\quad D = \frac{t}{\sqrt{\Sigma x\ (\text{or } n\bar{x})}} \quad (t \cong 2.0 \text{ for } 95\% \text{ probability of } D)$$

where D = index of precision, t = appropriate value from the Student's t-distribution for a defined probability level, and Σx = total number of individuals counted for a given taxa (Elliott 1977).

Results and discussion — Apparatus and procedure — The subsampling apparatus consists of a graduated plastic Imhoff settling cone (1 L) fitted with an aquarium air stone sealed into the bottom and connected to a compressed air supply. The entire apparatus is supported by a laboratory ring stand (Fig. 1).

The performance of the subsampler was tested using five replicates of three types of macroinvertebrate samples: stream benthic, stream drift, and pond benthic. Initially, the organic

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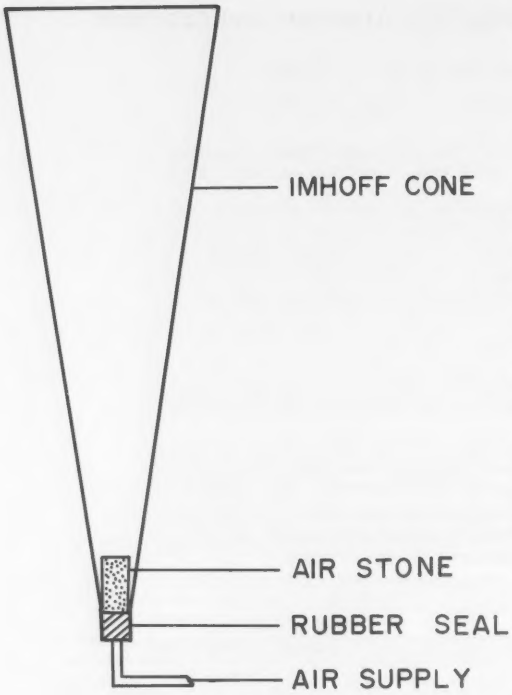

FIG. 1. Subsampler.

fraction of each sample was elutriated from the substrate using a bucket swirling technique (Needham and Needham 1962), although automated procedures (Lauff et al. 1961; Cross and Minns 1969; Pauly 1973; Worswick and Barbour 1974; Stewart 1975) could have been used. Following the protocol of Allanson and Kerrick (1961), the organic component was split into coarse and fine fractions using sieves. Large organic materials including filamentous algae were removed with the coarse sieve, leaving a homogeneously sized material for subsampling in the fine fraction. The organisms remaining in the coarse fraction were sorted and counted.

Subsampling was accomplished by placing the fine fraction into the cone and filling the apparatus to a total volume of 1 L, followed by agitation for 2–5 min to ensure thorough mixing. Care must be taken to regulate the flow rate of the air supply so that damage or fragmentation of delicate Ephemeroptera and Oligochaeta does not occur. Twenty-five percent of the original sample volume was subsampled by removing five subsamples from the agitated solution using a 50-mL test tube.

Random mixing of the macroinvertebrates was consistently achieved with the subsampler from both lentic and lotic (Table 1) samples. Because the subsampler is cone shaped, all of the material falls back towards the air stone at the bottom (Fig. 1), which resuspends the particles while simultaneously breaking up clumps creating a homogenous, randomly mixed suspension. By design, this alleviates the problem that Hickley (1975) indicates to be the major deficiency with most subsamplers, in that macroinvertebrates do not remain in suspension easily, and frequently entangle with one another or detrital material.

As the subsample counts conformed to a Poisson series, the Poisson distribution and its related statistics were used as a suitable model for estimating total numbers and associated 95% confidence limits of each taxon in the samples.

Statistical protocol — When the distribution of the macroinvertebrates in a subsampler has been shown to follow a Poisson series, the degree of precision of the estimated total count for a given taxon is dependent upon the total number of individuals counted, rather than the number of subsampling units taken. The precision estimate varies indirectly with the square root of the total count (Eq. 2), resulting in the percentage error of the count being an exponentially decaying function requiring four times the number of individuals counted for a twofold increase in precision (Fig. 2) (Lund et al. 1958). The rate of decrease in the percentage error of the estimate changes quickly with increased counting when $\Sigma x < 50$; however, when $\Sigma x > 50$ the improvement in the error term with increased effort is less rapid (Fig. 2).

When testing for randomness (Eq. 1), the calculation must always be made on at least five subsampling units (i.e. 4 df) (Lund et al. 1958; Elliott 1977). Additionally, for any given sample type, the mixing performance should be examined on a minimum of five replicate samples to establish randomness. Once randomness is demonstrated for a substrate type, as few as one subsampling unit needs to be taken for estimating the density and confidence limits (C.L.) of the macroinvertebrates in the total sample. The number of individuals to count for a desired degree of precision can be estimated from Fig. 2 or Eq. 2.

Hickley (1975) and Elliott (1977) have advocated that a sufficient number of subsamples be removed to ensure a count of at least 100 individuals to deem the subsampling method successful (i.e. ±20% precision at 95% C.L.). It would be desirable to achieve always an abundance estimate that is within ±20% of the true count. However, this rule generally restricts itself to samples with abundant taxa, where the density of organisms extracted within each subsampling unit requires only a few subsamples to be processed for the desired degree of precision. Adhesion to this rule would thus preclude the use of subsampling on community samples where abundance estimates of both common and rare taxa are required.

A suggested protocol for dealing with community samples is to predetermine the number of subsampling units to be taken (minimum of five recommended). The disadvantage of this approach is that processing effort may be more than required for some taxa (i.e. >100 individuals counted). This problem can be overcome by enumerating abundant taxa in the number of subsampling units required to achieve the desired degree of precision and subsequently ignoring them in remaining subsamples. Quantification of the rarer taxa would be based upon processing all of the subsamples, with additional subsamples being taken if the associated error terms (calculated using Fig. 2 or Eq. 2) were not acceptable.

Applying this procedure, general trends between samples (Table 1) were ascertained despite some taxa displaying large error terms caused by low counts. As Lund et al. (1958) indicated, most ecological studies are concerned with changes

TABLE 1. Subsample counts obtained for each taxon occurring in five lotic, benthic, and drift samples and calculated Index of Dispersion (I), total counts, and percentage error of estimates.

Sample type	Taxon	Sample no.	Subsample 1	2	3	4	5	I	Total	% error (95% C.L.)
Benthic	Baetidae	1	16	11	3	11	12	8.42	53	27
		2	0	1	5	3	3	6.33	12	58
		3	3	5	3	3	3	0.94	17	49
		4	15	10	11	14	25	9.47	75	23
		5	5	5	6	5	2	2.00	23	42
	Chironomidae	1	33	20	23	31	23	4.92	130	18
		2	41	35	39	28	20	9.12	163	16
		3	33	34	44	42	33	3.09	186	15
		4	47	59	47	52	67	5.43	272	12
		5	57	71	47	54	59	5.33	288	12
Drift	Baetidae	1	6	3	5	3	3	2.00	20	45
		2	4	8	9	8	4	3.52	33	35
		3	15	14	18	12	15	1.27	74	23
		4	5	6	4	11	8	4.53	34	34
		5	8	13	7	8	11	2.68	47	29
	Leptophlibidae	1	4	4	5	3	3	0.74	19	46
		2	5	4	6	3	1	3.89	19	46
		3	40	41	27	30	36	4.33	174	15
		4	9	6	6	5	6	1.44	32	35
		5	6	6	8	4	4	2.00	28	38
	Chironomidae	1	12	19	24	23	16	5.26	94	21
		2	14	19	19	15	16	1.28	83	22
		3	58	44	48	57	49	2.87	256	13
		4	30	46	32	34	25	2.00	167	15
		5	30	29	37	26	33	2.26	155	16

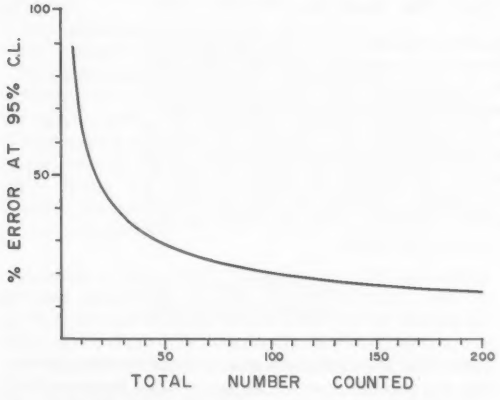

FIG. 2. Relationship between the total number of individuals counted in the subsample(s) and the associated percentage error at a 95% probability level.

in population abundances of greater than 100%, in which case an estimate of abundance to an accuracy of ±50% (a total count of only 16 at 95% C.L.!) would be sufficient to observe any trend.

The choice of approach therefore becomes dependent upon the ecological question being asked. When accurate population density estimates are required, if possible, a sufficient number of subsamples should be processed that will result in total counts having low associated error terms. Conversely, if general trends in community composition and abundance are being examined on a spatial or temporal basis, using the approach of standardizing the number of subsamples taken would be adequate.

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Relationship of Fishing Mortality to Natural Mortality and Growth at the Level of Maximum Sustainable Yield

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DERISO, R. B. 1982. Relationship of fishing mortality to natural mortality and growth at the level of maximum sustainable yield. Can. J. Fish. Aquat. Sci. 39: 1054–1058.

Fishing mortality constraints are derived for fishes harvested at the maximum sustainable yield (MSY) determined by a delay-difference population model. Those constraints depend upon rates of natural mortality and growth as well as a simple constraint placed on abundance of the exploited population. The results are generalized for a wider class of population models where it is shown that MSY fishing mortality is constrained often to be less than the fishing mortality which maximizes yield per recruit. Fishing mortality rates are lower in the delay difference model in comparison to MSY fishing rates in the logistic model, when a quadratic spawner–recruit curve is applied.

Key words: delay-difference model, logistic model, fishing mortality, maximum sustainable yield, yield per recruit

DERISO, R. B. 1982. Relationship of fishing mortality to natural mortality and growth at the level of maximum sustainable yield. Can. J. Fish. Aquat. Sci. 39: 1054–1058.

On détermine les contraintes de la mortalité due à la pêche pour les poissons pêchés au rendement maximal soutenu (RMS) établi par un modèle de population à variables retardées. Ces contraintes dépendent des taux de mortalité naturelle et de croissance ainsi que d'une simple contrainte placée sur l'abondance de la population exploitée. Les résultats sont généralisés pour une plus grande classe de modèles de populations où il est démontré que la mortalité due à la pêche à un rendement maximal soutenu est souvent restreinte à une valeur moindre que la mortalité due à la pêche qui maximise le rendement par recrue. Les taux de mortalité due à la pêche sont moins élevés dans le modèle à variables retardées que les taux de pêche à un rendement maximal soutenu du modèle logistique, quand une courbe quadratique des recrues en fonction des géniteurs est mise en application.

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POPULATION parameters often are not available for many aspects of fish population dynamics important for quantifying maximum sustainable yield (MSY). As a consequence, fishing mortality (MSY level) has been assumed by certain writers (Alverson and Pereyra 1969; Gulland 1970) to be equal to the natural mortality rate. That equivalence has been shown (Francis 1974) to be false under most conditions in a logistic stock production model, leaving fisheries managers without means of approximating MSY exploitation for fishes where little is known about their spawner–recruit relationship. It is possible, however, to place an upper bound on MSY exploitation.

This paper is devoted to an examination of constraints on fishing mortality imposed by natural mortality and growth when simple constraints are placed on the abundance of the exploited population. A delay-difference population model presented in Deriso (1980) is the principal one used in this analysis, although some characteristics of a logistic model are given to gain additional insight, and generalizations are made to a wider class of population models. A limitation of the treatment present here is that density-dependence in survival

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and growth of a year-class is assumed to occur prior to age of recruitment into the fishery.

Population model equations — The delay-difference model of Deriso (1980) for an exploited, seasonally breeding population with knife-edge recruitment into the fishery can be written as

$$(1)\quad B_{t+1} = (1+\rho)\,\ell S_t - \rho\ell^2 \frac{S_t}{B_t} S_{t-1} + F(S_{t+1-k})$$

where ℓ = annual natural survival fraction for adults $[\ell = \exp(-M)]$

ρ = Brody's growth coefficient for weight

B_t = biomass of the catchable population in year t

C_t = annual catch in biomass

$S_t = B_t - C_t$ = escapement of catchable adults

k = age of recruitment in the fishery

$F(\cdot)$ = spawner–recruit relation for biomass of recruits.

Other parameters used in this paper include

$f_t = C_t/B_t$ = annual exploitation fraction of biomass $[f = 1 - \exp(-F)]$

$\text{rv} = [(1-\rho\ell)(1-\ell)]^{-1}$ = reproductive value (in units of biomass per unit biomass) of age k recruits in the unfished (virgin) population

$\text{rv}^* = (1-f)\{[1-\rho\ell(1-f)][1-\ell(1-f)]\}^{-1}$ = reproductive value of age k recruits in the exploited population.

The logistic model, analogous to that in Francis (1974), is given as

$$(2)\quad \frac{dN}{dt} = (\alpha - \beta N)N - MN - FN$$

where $(\alpha - \beta N)N$ = spawner–recruit relation for number of recruits

M = annual natural mortality rate

F = annual fishing mortality rate

N = number of individuals in the population.

Exploitation is treated differently in these two models. In the logistic model, the exploitation fraction is assumed to be a consequence of competing mortality rates of fishing and natural sources, whereas, in the delay-difference model in this paper, fishing and natural mortality are assumed to be sequential, nonoverlapping events — a reasonable assumption for seasonal fisheries.

Analysis of equilibrium exploitation — The relationship between exploitation, growth, natural mortality, and the spawner–recruit equation can be examined by solving for MSY in the delay-difference model (1). That solution was derived in Deriso (1980, equation 6) and can be written as

$$(3)\quad \text{rv}\,\dot{F}(S_e) = 1 - \rho\ell^2\,\text{rv}\,f^2$$

where $\dot{F}(S_e)$ = slope of spawner–recruit function $F(\cdot)$, evaluated at equilibrium escapement S_e.

The slope $\dot{F}(S_e)$ is greater than (or equal to) zero for most MSY solutions. The property of nonnegative slope is equivalent to requiring that MSY occurs for spawning stock sizes less than (or equal to) that which produces maximum recruitment; for semelparous populations ($\ell = 0$), that property always holds true. That property is also equivalent to requiring that recruitment at MSY not lie on the declining limb of a spawner–recruit curve. Analysis later in this paper shows the type of conditions that violate the property of nonnegative slope.

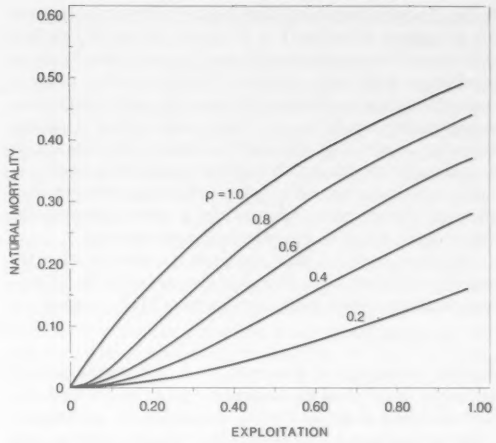

FIG. 1. Upper bounds on exploitation (f) are displayed for various growth (ρ) and natural mortality ($1 - \ell$) parameter values.

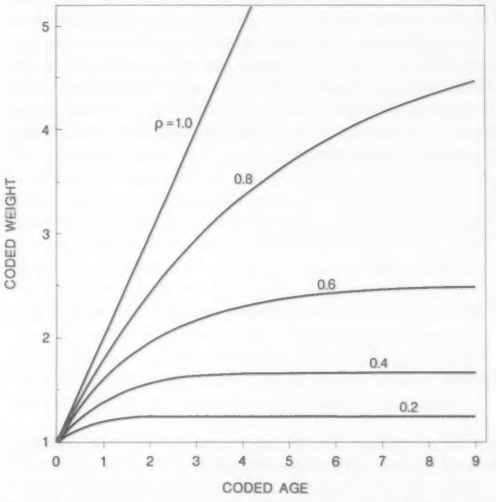

FIG. 2. Growth patterns predicted by the Brody growth equation in the delay-difference model (1). Coded weight is defined as weight of an animal at a given coded age divided by weight of the animal at recruitment age. Coded age equals age of animal minus age at recruitment into the fishery.

By requiring that the property ($\dot{F}(S_e) \geq 0$) hold true, an upper bound for exploitation can be derived. Here the right-hand side of equation (3) can be rewritten:

$$(4)\quad f \leq \sqrt{\frac{1}{\rho\ell^2\,\text{rv}}}.$$

In Fig. 1 upper bounds on f are displayed for various growth (ρ) and natural mortality ($1 - \ell$) values. Values of f are less constrained for populations with small ρ values than for those populations with large ρ values. Fishing mortality is never constrained to be less than natural mortality, although they are approximately equal for $\rho = 1$ and small values of natural mortality. Figure 2 is included to enhance visualization of the pattern of growth in fish implied by different ρ values — small ρ values correspond to fishes with little growth potential after age of recruitment, whereas high ρ values correspond to fishes with substantial growth after recruitment age.

The slope, rv $\dot{F}(S_e)$, must always be less than (or equal to) one for a MSY solution. Therefore, we can write the following inequality, which holds true for most MSY solutions:

$$0 \leq \text{rv } \dot{F}(S_e) \leq 1.$$

A slope at midpoint in that range (rv $\dot{F} = \frac{1}{2}$) corresponds to an f equal to $1/\sqrt{2}$ of the maximum f given by equation (4). And for a large slope (rv $\dot{F} = \frac{3}{4}$), f equals $\frac{1}{2}$ of the maximum f.

Let us examine a specific spawner–recruit curve to gain further insight into properties of MSY solutions. The quadratic equation $(\alpha - \beta S)S$ of the logistic model (2) provides a spawner–recruit curve that can be used to compare results of model (2) with those of model (1). That quadratic equation has two intercepts (0, α/β) with maximum recruitment at $S = \alpha/2\beta$. Let us introduce a proportionality constant, c, where $Sm = c\alpha/\beta$; Sm denotes spawning stock size in the unexploited population. Values of c close to one correspond to high density-dependence in survival of recruits, as recruitment is zero at $c = 1$. Under no exploitation, equilibrium of model (1) occurs when

$$\text{rv}(\alpha - \beta Sm) = 1$$

therefore,

$$\alpha = \frac{1}{\text{rv}(1 - c)}.$$

Under exploitation, equilibrium of model (1) occurs when

$$\text{rv}^*(\alpha - \beta S_e) = 1$$

so that

$$\beta S_e = \alpha - 1/\text{rv}^*.$$

By differentiating the quadratic spawner–recruit equation and substituting the results, we obtain

$$\text{rv } \dot{F}(S_e) = \text{rv}(\alpha - 2\beta S_e) = 2\frac{\text{rv}}{\text{rv}^*} - \frac{1}{1 - c}.$$

After equating the solution (3) with the above equations, we obtain a characterization of MSY solutions:

$$(5) \quad 2\frac{\text{rv}}{\text{rv}^*} - \frac{1}{1 - c} = 1 - \rho\ell^2 \text{ rv } f^2.$$

Equation (5) can be used to examine other aspects of MSY solutions. Upper bounds of the proportionality constant c were calculated in (5) and listed in Table 1; rv $\dot{F} \geq 0$ for c values less than those upper bounds, irrespective of the natural mortality coefficient. As seen in Table 1, recruitment in the unexploited population must be severely depressed (large c value) for MSY to occur when rv $\dot{F} < 0$. Table 1 also includes upper bounds on constant c for other slopes (rv $\dot{F} = \frac{1}{2}$, rv $\dot{F} = \frac{3}{4}$); severely depressed recruitment in the unfished population is indicated for slopes as small as three-quarters (i.e. where f is one-half the upper bound given by equation (4)).

TABLE 1. Upper bounds on proportionality constant c that insure rv $\dot{F} \geq 0$ for various growth fractions.

Growth (ρ)	Upper bound on constant c: for slope = 0	for slope = $\frac{1}{2}$	for slope = $\frac{3}{4}$
0.2	0.98	0.96	0.92
0.4	0.95	0.92	0.87
0.6	0.93	0.89	0.83
0.8	0.91	0.86	0.79
1.0	0.88	0.82	0.74

Let us examine briefly properties of the logistic model (2) to gain other perspectives about MSY. Terminology given in Francis (1974) is used here: N_m is the number of individuals in the unexploited population; N_e is the number of individuals at equilibrium; F_{op} is the fishing mortality rate at MSY. First, we show that the slope of the quadratic spawner–recruit curve at MSY is nonnegative. Francis (1974) has shown that $2F_{op} + M = \alpha$ and that $N_e = F/\beta$. We see that $N_e < \alpha/2\beta$ (where the maximum recruitment occurs) because the following inequalities hold at MSY:

$$N_e = F_{op}/\beta < F_{op}/\beta + M/2\beta = \alpha/2\beta,$$

and, therefore, the slope of that spawner–recruit curve is positive at MSY. A relationship exists between F_{op} and M which depends on the proportionality constant c, where $N_m = c\alpha/\beta$. Because $N_m = (\alpha - M)/\beta$, we find that

$$\alpha = M/(1 - c)$$

Therefore,

$$F_{op} = (\alpha - M)/2$$

$$= \frac{c}{1 - c}\left(\frac{M}{2}\right).$$

The following correspondences can be derived from the equation above.

$F = M$ when $c = \frac{2}{3}$

$F = M/2$ when $c = \frac{1}{2}$

$F = \dfrac{3M}{2}$ when $c = \frac{3}{4}$.

Fishing mortality rates are substantially lower in the delay-difference model than would be indicated by the logistic model for given values of proportionality constant c. Table 2 lists minimum and maximum values of f as a function of natural mortality and constant c; that range of f values corresponds to a range of growth ρ values ($\rho = 0.1$ to $\rho = 1.0$) where minimum f applies to $\rho = 1.0$ and maximim f applies to $\rho = 0.1$. Exploitation fraction is less than natural mortality in Table 2, except for one case with the combination of low growth (small ρ), small natural mortality, and large c value (severe depression of survival of recruits in the unexploited population).

TABLE 2. Range of exploitation fractions (f) corresponding to a range of growth values ($\rho = 0.1$ to $\rho = 1.0$) and specified natural mortality ($1 - \ell$) and constant c.

Natural mortality	Range of MSY exploitation fractions: for $c = \frac{1}{2}$	for $c = \frac{2}{3}$	for $c = \frac{3}{4}$
0.2	0.05–0.09	0.08–0.16	0.11–0.22
0.4	0.10–0.16	0.18–0.28	0.24–0.36
0.6	0.17–0.23	0.29–0.37	0.37–0.47
0.8	0.25–0.28	0.39–0.44	0.49–0.54

Generalization and application of the MSY fishing mortality constraint — Fishing mortality constraints can be generalized to a wide class of population models. Let us restrict our attention to models with the following two attributes: (i) equilibrium recruitment (R) is a function of spawners (S_e) with the spawner–recruit function $R = F(S_e)$, and (ii) spawners at equilibrium equals escapement from the fishery of biomass of individuals from age of recruitment and older, $S_e = B - C$. To characterize maximum sustainable yield, let us define our control variable as the exploitation fraction f where $C = fB$. Our problem is to maximize C by varying f. Hence we have the necessary condition

$$\frac{dC}{df} = 0$$

and by partitioning C as $(C/R)R$, we obtain the equivalent condition

$$R \cdot \frac{d(C/R)}{df} + (C/R) \cdot \frac{dR}{df} = 0.$$

It is straightforward to show that $\frac{dR}{df} \leq 0$ when $\dot{F}(S_e) \geq 0$. And in this case we obtain the result that

$$(6) \quad \frac{d(C/R)}{df} \geq 0.$$

We recognize the ratio (C/R) as being the yield per recruit obtained with exploitation f. Commonly used yield per recruit equations (such as the year-class model of Beverton and Holt 1957) are unimodal functions of f so that the largest value of f which satisfies equation (6) is obtained at the point of equality in (6). This point of equality characterizes the f that maximizes yield per recruit. We can summarize this result as follows,

$$(7) \quad f(\text{MSY level}) \leq f(\text{maximum yield per recruit})$$

where the f for maximum yield per recruit satisfies $d(C/R)/df = 0$. The delay-difference model (1) contains a unimodal yield per recruit relationship so that the upper bound in equation (4) represents the exploitation that maximizes yield per recruit in that model.

The results of this paper can be applied to obtain a reasonable upper bound on MSY exploitation for many fish populations. Yield per recruit analysis using a procedure, such as the Beverton and Holt year-class model with age of recruitment set at age of sexual maturity, provides such an upper bound for MSY fishing mortality. However, to illustrate the applicability of equation (4), estimation of this constraint was made for Pacific halibut of the northeast Pacific Ocean. The first step is to obtain an estimate of the growth parameter ρ, subject to the constraint that it lies in a feasible range $(0 \leq \rho\ell < 1)$ for model (1). This estimate, $\hat{\rho} = 0.97$, was obtained by a nonlinear least squares procedure applied to the Brody weight equation (equation (1) of Deriso 1980) for samples of average weight of halibut (ages 8–20 yr) caught during the years 1976–80. An alternative procedure can be applied by recasting the Brody equation in a linear form (page 222 of Ricker 1975, where $\rho = k$ in Ricker's notation and w_t replaces l_t in Ricker) and using linear regression to obtain $\hat{\rho} = 1.03$. The simple procedure of estimating ρ by equating $(\rho = 1 - w_t/w_\infty)$ as shown in Deriso (1980) is reasonable for providing a coarse estimate. A precise estimate of ρ is needed for age-classes prevalent in the fishery, however, so that this last procedure is not recommended in application. The second step is to obtain an estimate for ℓ and, because $M = 0.2$ is commonly used for halibut, we obtain $\hat{\ell} = 0.82 = \exp(-0.2)$. The inequality (4) takes the form $f \leq 0.24$ by substituting $\hat{\rho} = 0.97$ and $\hat{\ell} = 0.82$ into (4) and into the equation for reproductive value (rv). Recent estimates of equilibrium yield of halibut of the northeast Pacific (IPHC 1981) correspond to $f = 0.12$, based on estimates of combined incidental and equilibrium commercial catch, and on estimates of adult halibut abundance presented in that document.

In summary, the upper bound on MSY exploitation given by formula (4) is applicable for most fish populations; the exceptions are those which exhibit extreme depression of recruitment in their virgin (unexploited) state, according to analysis of a quadratic spawner–recruit curve. Analysis of that quadratic curve demonstrated that the upper bound of exploitation in equation (4) can be reduced by 50% and still remain valid for populations without severe depression of recruitment in the virgin state. Fishing mortality rates obtained from analysis of the delay-difference model were smaller than those obtained with a logistic model; fishing was less than natural mortality for most of the model (1) cases considered. Formula (4) was found to have a direct analog in a wider class of population models where it was shown to be equivalent to the more general statement: MSY exploitation is less than (or equal to) exploitation that maximizes yield per recruit when conditions specified above formula (7) are met.

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PERSPECTIVES

Ocean Sciences in Relation to Living Resources

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The Intergovernmental Oceanographic Commission's Resolution XI-17 on Ocean Sciences in Support of Living Resources specifies that programs should be formulated in applied ocean research related to fishery problems. In this report we identify some types of needed research. We discuss the relative importance of the various life history stages to the question of resource variation regarding difficulties in sampling or studying on relevant scales. Our report stresses identification and accounting for causal climate-driven ambient variations. Some testable hypotheses relating the larval stages are given as examples of useful research. We also describe research needed on predation and species interactions. Examples of specific systems where important ecological processes need intense study are given. Upwelling areas, coral reefs, tropical and shelf demersal fisheries, and the open ocean fisheries each require different types and scales of study. The importance of data accessability and multidisciplinary research activities, beginning with dialogues between the ocean research and fishery resource scientists is paramount to successful completion of these tasks. The examples provided may stimulate further effort to identify resource research problems and programs for resolving them.

Key words: ocean science, living resources, life history cycles, fishery recruitment, predation, species interactions, fish eggs and larvae, vertical stability of the ocean, advection, convergence and divergence, upwelling systems, coral reefs, tropical demersal fisheries

BAKUN, A., J. BEYER, D. PAULY, J. G. POPE, AND G. D. SHARP. 1982. Ocean sciences in relation to living resources. Can. J. Fish. Aquat. Sci. 39: 1059 – 1070.

La résolution XI-17 de la Commission intergouvernementale d'océanographie concernant les sciences océaniques à l'appui des ressources vivantes spécifie qu'il faudrait formuler des programmes de recherche océanologique appliquée axés sur les problèmes de la pêche. Le présent rapport identifie quelques genres de recherches nécessaires. On traite de l'importance relative des diverses étapes du cycle évolutif dans la variation de la ressource, en ce qui a trait aux difficultés d'échantillonnage ou d'étude sur une échelle appropriée. Le rapport met l'accent sur l'identification et l'explication des variations ambiantes causales qu'entraîne

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le climat. Quelques hypothèses vérifiables établissant un rapport entre les stades larvaires sont donnés comme exemples de recherche utile. On décrit aussi la recherche nécessaire sur la prédation et l'interaction des espèces, et on donne des exemples de systèmes spécifiques nécessitant une étude intense des principaux processus écologiques. Les zones de remontée d'eau profonde, les récifs de coraux, les pêches démersales dans les tropiques et sur la plate-forme continentale, et les pêches en haute mer nécessitent des recherches de types et d'échelles différents. La facilité d'accès des données et des activités de recherche multidisciplinaire, débutant par des dialogues entre les scientifiques en recherche océanique et les scientifiques en ressources halieutiques, sont d'une extrême importance pour l'achèvement de ces tâches. Les exemples fournis peuvent stimuler des efforts supplémentaires pour identifier les problèmes de recherche sur les ressources et les programmes pour résoudre ceux-ci.

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Background to the Report

At its 11th Assembly the Intergovernmental Oceanographic Commission (IOC) passed Resolution XI-17 on Ocean Sciences in Support of Living Resources (OSLR). The purpose of this resolution was to promote development of plans for major oceanographic studies of the physical–ecological interactions of importance to fishery resource-related problems for submission to the 12th Assembly in 1982. IOC and the Food and Agriculture Organization (FAO) appointed two rapporteurs, Dr T. Austin and Dr J. A. Gulland, respectively. In consultation with the IOC Secretariat, they decided that the most useful approach was to convene a small group of individuals actively involved in research on multispecies and climate–environment physical processes applied to fisheries problems, which could provide a useful survey of present-day thinking on how to begin formulating such plans. This document, originally identified as the Report of the "Group of Four," was circulated widely throughout the oceanographic community as a stimulus for comments and a basis for thoughtful progress toward the objectives of the OSLR resolution.

The fact that both distributions and abundances of resource species are related directly to environmental properties such as temperature, food, and oxygen is of primary importance. However, few well-defined examples are available of direct causal relationships between variations in abundance and environmental processes beyond the seasonal "displacement" of the above properties or observations of nonusual events relative to some geographic base (i.e. North Atlantic cooling trend and cod occurrence).

Much of our ignorance in this regard can, I believe, be attributed to wrong-scale thinking. For example, studies of recruitment of fishes often integrate the entire early life history of these fishes into a single prerecruit class, and the relations between recruitment and subsequent production are sought from trying to match up only spawning biomass and recruits, with the residuals or deviations from any one of the numerous available stock–recruitment formulations being attributed to "environmental variations." The major proportion of the mortalities in most oviparous species occur in the prerecruit stages. The order of magnitude of the recruitment is therefore primarily dependent upon variations in about the 4th or 5th decimal place in these day-by-day, stage-by-stage probabilities of survival.

The single, most important distinction in the recently emerging approaches to these problems of recruitment is the idea that there are very important processes at scales relevant to survival of *individual* fish larvae and juveniles which must be encountered, or the larvae cannot survive. This implies that there are hierarchic hurdles to be faced resulting in variable and discontinuous mortalities rather than averages or constants.

Much of this current thinking is described for the problems of dealing with only first feeding of pelagic fish larvae in IOC Workshop Report No. 28 on the effects of environmental variation on the survival of larval fishes (1980). Increasing our knowledge of the trophic levels supporting this single stage and beyond will require intense multidisciplinary study.

The significance of environmental variability on the numerous trophic levels is the subject of many biological oceanographic studies. These often elusive intricacies of marine ecosystems are driven by solar energy which generates climatic events arising from diurnal, seasonal, and epocal processes of energy absorption, transfer, and dissipation, often months and thousands of kilometres away (i.e. El Niño) as well as daily, local events (i.e. insolation, wind, rainfall).

One major problem is our need to develop methods for measuring and monitoring directly or via proxies (i.e., upwelling or stratification indices) the directly causal processes important to the variations in survival of the numerous fishery resources. This means that appropriate scales need to be defined, that appropriate measurements be identified, and that sensors and equipment should be designed and employed to resolve these processes into useful signals.

Equally important is the training of fishery and oceanographic scientists in the principles and use of the sensors and equipment, long-term data collection, and the employment of cause-and-effect (or rational) hypothesis testing. This will certainly include experimental research in the laboratory as

well as on the sea so as to provide evidence that there are true cause-and-effect linkages between the various important signals.

For example, without the fruitful, diligent research of many of the co-workers in Lasker's Laboratory, his hypothesis regarding the importance of small-scale phytoplankton stratification in the larval habitat to the survival of the California Anchovy (Lasker 1975) and other important pelagics might have remained speculative. However, the laboratory studies of Hunter (1972, 1976), Hunter and Thomas (1974), Arthur (1976, 1977), Lasker and Zweifel (1978), O'Connell (1976, 1980), O'Connell and Raymond (1970), and Methot and Kramer (1979) have provided supportive evidence for Lasker's hypothesis. They have also helped further define appropriate scales of sampling at sea and in the laboratory for improving our understanding of the conditions promoting survival of individual larval fishes in the sea.

From this same research group we have learned about rates of important egg and larval fish mortality processes due to cannibalism (Hunter and Kimbrell 1982), spawning site selection and predation (Alvariño 1980), and the significance of batch fecundity (Hunter and Goldberg 1980) to the interpretation of conventional egg and larval surveys.

In particular the California northern anchovy (*Engraulis mordax*) examples are stimulating, formative observations, employing new and classical methods yielding interactive research results from which we can begin to challenge the overintegrative "conventional wisdoms."

This extreme case of "focused" research could lead one to conclude that to investigate each important commercial species would require unlimited resources and expertize. In fact, this is not true. These examples provide numerous opportunities to test quickly or evaluate generalities of such fundamental processes as first feeding which must certainly be a common property of newly hatched fishes, onward through ecological and environmental properties which promote, or subsequently fix the limits of survival into the following stages or ecological challenges. Once a decision regarding causal processes has been reached, appropriate proxies can be identified and monitored on relevant scales.

These and many similar experiences have led to the formulation of this report.

As the experimental research activities in the world ocean become more restricted because of conflicts of interest and jurisdictional progress, it seems that both the applied and academic scientists will of necessity recognize their interdependence, even to the point of initiating required dialogues and mutual-objective research. The relative isolation which has been characteristic between marine science and fishing-related problems needs to be diminished. This has been said by so many for so long that it must be a real problem. OSLR is an opportunity for scientific collaboration, mutual dialogue and familiarization, and resolution of important worldwide problems. OSLR is both challenging and sobering. Perhaps OSLR will provide stimulus for the maturity of marine ecological research into the fruitful and valuable applied science it should become.

The Group met at FAO Headquarters, Rome, Italy (Fisheries Department), from October 14 to 17, 1980, and included the following persons: A. Bakun, J. Beyer, D. Pauly, and J. G. Pope (Chairman) as members of the 'Group of Four Scientists.' The two previously mentioned rapporteurs; G. Tomczak, IOC Secretariat; G. D. Sharp, FAO Fisheries Resource and Environment Division; H. Austin and FAO staff also took part in the discussions.

Obviously readers will recognize that so few people in so short a time could not address the problem in more general terms and still have something tangible for others to add to, or assault, as the case might be. Stimulation was the objective; problem definition and resolution is the product expected from the readers.

G. D. SHARP

The Report

Introduction

The Group decided to confine its discussions to ocean areas between 45°N and 45°S to focus attention on the fisheries problems of the developing world. This document was an attempt to identify gaps in our knowledge of important fisheries-related processes which might be closed, given the attentions of the ocean sciences, in the broadest sense. The Group saw many areas where research would be valuable. However, we noted that for this research to be useful in understanding fisheries problems, it would need to be conducted on a time-and-area scale appropriate to the fishery in question.

The Group agreed that oceanic research of all sorts was potentially valuable; however, for direct use, ocean research in support of resource science argues for close collaboration between fisheries and other ocean scientists at all stages of research.

Problems of fishery science arise from the need to answer questions posed by the fisheries management community, particularly in the face of the numerous conflicts of interests, i.e. among different methods of commercial fishing or commercial fishing vs. sport fishermen, or subsistence fishermen vs. public opinion, and, most important, restrictions imposed as conservation measures vs. exploitation interests. Some of these questions can be answered by the collection and interpretation of fisheries data (catch, effort, age structure data, etc.) but others have proved intractable on this basis. From experiences in well-studied areas such as the North Sea, California, and the waters around Japan, it is clear that problems of recruitment, availability, and species interactions cannot be solved from fisheries data alone.

Some conventional fishery-related questions generally asked and the problems posed are set out below:

Management tasks from the FAO perspective	*Empirical approaches and scientific problems*
1) For a region where fisheries are not fully exploited: identify the resource(s), describe their seasonal and long-term distribution patterns, and evaluate possible effects in neighboring fisheries.	Survey or exploratory fishing, comparison with data sets from known area, identify unconventional resources, identify efficient harvest methods.
(2) For a growing fishery: determine potential yield and its likely variability.	Identify population characteristics and population structure, estimate present abundance, investigate ecological interactions, compare natural and man-induced variations within and outside of area.
3) For both developing and developed fisheries: improve operating efficiency.	Locating fish stocks and their seasons and areas of vulnerability; investigate source of variance in vulnerability, including those that are due to environmental fluctuations; predict catches.
4) For a fully exploited fishery: set suitable constraints to achieve rational exploitation:	
a) For single species with uniform recruitment.	Estimate population parameters such as growth rate, onset of maturity, mortality rates at various stages.
b) For single species with variable recruitment.	Factors affecting recruitment, including minimum spawning biomass. Early estimation of year-classes.
c) For fisheries on several species.	Effects on one species of changing patterns of fishing on other species.

The problems relating to the first two questions are concerned with fisheries development. They are thus transitory problems which need coarse but timely advice. In many cases order of magnitude answers would be sufficient. Questions of operational efficiency and management, however, are permanent features of fisheries requiring more accurate advice which may be developed over a longer time frame. Operational questions may need to be answered to within a factor of 2 while management questions ultimately need to be understood with greater precision.

For these reasons the problems associated with questions of fisheries operations and management seem the most appropriate for the inputs of longer term scientific advice. The problems of (1) Availability (distribution, abundance, vulnerability to gears), (2) recruitment and life cycle or natural history variations, and (3) species interactions are the problems which seem most pressing in well-studied fisheries; however, this may not be the case for all systems. Therefore, the report considers questions arising from various stages of fish life cycles and also problems arising in the major ecological systems associated with the developing world. The proposed types of research at the locations suggested are in no way intended to be exhaustive. Rather they are in the nature of examples of what might be done.

Life History Cycle

Definitions of Life History Stages

The common denominator in the world major food fish resources is that oviparous fishes dominate the catches. Only a few exceptions are notable, i.e. *Sebastes* species, elasmobranchs, *Zoarces* species, etc. Therefore, in portraying a typical life cycle pattern it is appropriate to start with the egg in the water column and proceed by stages of development and characteristics of these stages toward the deposition of eggs in the subsequent generation. A simple circle diagram can be used to describe this pattern.

Stage I comprises entry of the egg into the environment (A), fertilization and subsequent prehatch larval development; hatching of the larvae (B) and subsequent development up through metamorphosis (C — loosely defined here as the time scales form or when dominant respiration switches to the gills).

Stage II includes the posttransformation developmental stages of juveniles (D) which precede entry of the fish into vulnerability to fishery operations (E). This is the least-understood stage in the life history cycle of many fish because there is no appropriate gear to sample them effectively during this stage.

Stage III includes the period from initial entry of the fish into the fishery or sampling operations (E), of juvenile to adult fishes before the onset of gamete maturation (F).

Stage IV is defined as that period from the onset of gamete differentiation and maturation (F) to the end of the reproductive period of the individual. This may be seasonal, annual, or continuing over varying time scales, depending upon the species. Also, egg maturation and subsequent spawning may happen once or several times in a lifetime, i.e. iterative within any year (Hunter and Goldberg 1981) or annual.

Life cycles determine susceptibility of the populations to short and longer term system variations, physical and/or ecological in nature. Early life history stages exhibit variations based on, for example, temperature or food conditions.

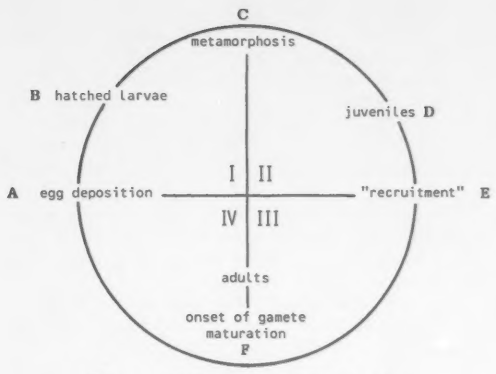

FIG. 1. A schematized life cycle of fishes.

"Ecological positions" shift continuously as fish grow, but these shifts are different, i.e. have differing rates of change, within and among species, and represent responses to system changes. Obviously death may occur at any point in the diagram.

A common starting point for oviparous species is the hatched larvae's need to encounter appropriate densities of appropriate foods to stimulate first feeding (from B on the diagram). The larvae that are *not placed* into the appropriate environment do not survive. Appropriate survival environments are 'windows' in time and space. They are probably not forecast by the adults in any direct sense in many coastal fishes. This is evidenced by their long or continuous spawning seasons. Other species having localized spawning (e.g. homing) and short reproductive seasons are tuned to relatively stable systems which are found to vary on the decade time scale as these populations also do (Iles and Sinclair 1982). More complicated reproduction behaviors are expected in the open ocean (oceanic) species because the patchiness and availabilities of species-specific "survival windows" may be on different and probably extensive time and area scales in the oceanic systems (Sharp 1981). These species must have a more definite ability to identify "appropriate larval survival habits" than the other species or there are more of these densely populated larval fish nurseries than is presently suspected.

The upper quadrants (I and II) of Fig. 1 represent stages in which survival is only rarely affected by man directly (except for pollution and habitat destruction). All stages are directly affected by environmental variations and this is the basis of several problems which could be tackled by scientific researchers.

Stage I — egg and larval survival — Extreme vulnerability and high rates of mortality characterize the egg and larval stage; this stage is considered the most critical to eventual recruitment. There are multiple interacting processes involved including feeding, growth, predation pressure, etc. at various substages. Because most of the available data are from the adult stage which is sampled by a fishery, it is a common practice to integrate the processes of Stage I, and of the juvenile stage (II) as well, by means of empirical stock–recruitment functions. Unfortunately these functions often provide poor fits to the observed data. The deviations are commonly attributed to environmental effects.

One way to view the problem is in terms of a multiple regression in which stock size (S) is included with environmental terms (E_i) as explanatory variables. For example, the formulation:

$$\log R/S = a_o + a_1 S + a_2 E_1 + a_3 E_2 + \ldots$$

is a Ricker (1975) function modified by environmental terms.

Obviously, if the dependence on S is less important than the environmental dependence, neglecting environmental terms leads to a poor estimate of the dependence on S (which is the only term that can be influenced by management). However, there is always an extremely limited number of data points available. Thus, the number of explanatory variables must be reduced to a minimum. This should be done on rational grounds, based on the best available understanding of cause–effect relationships between recruitment and environmental factors. Terms relating to multispecies interaction (for example, the size of a predator stock) might be incorporated similarly.

Such a procedure is an example of the combination of the rational (cause–effect) approach, which is based on understanding of the physical and biological processes involved, and of the empirical approach in which the functional relationships are defined by analysis (e.g. by regression) of available data. A strictly rational approach is usually not feasible. The complex linkages between environmental processes and biological consequences are extremely difficult to observe or to investigate experimentally; the quantitative information needed to construct rational models of those linkages is most often unavailable. On the other hand, the empirical approach is hampered by a lack of sufficient data points. Fishery data characteristically yield one estimate of stock size and recruitment per year; the available time series rarely exceed several decades and most often are of the order of 10–20 yr. To sort out a multitude of possible environmental effects by statistical means from a series of 10–20 data points is not possible. Moreover, the time series often contain significant autocorrelation, indicating a lack of independence of data points, which further reduces the limited degrees of freedom.

It is also important to realize that the concept of one single recruitment graph (deterministic approach) needs to be replaced by stochastic approaches that are based on probabilistic formulations of the endogeneous variables such as stock size variation, age structure variation, hence fecundity variation, etc. This is in contrast to exogenous stochasticity (i.e. forcing functions in terms of independent, random variations such as temperature patterns or turbulence-inducing events) which is useful for sensitivity analysis but otherwise usually of little value. The stochastic formulation allows for the possibility of expressing statements on recruitment in terms of probabilities.

Generally, a combination of the rational and empirical approaches allows a great amount of the limited information available to be incorporated. Often, the rational approach is used to generate hypotheses and to test and quantify those processes which can be measured or addressed experimentally. Then the empirical approach, i.e. experimental study, is used for testing, calibration, and verification. Further pro-

gress in fishery science requires advances in both approaches. A better rational, i.e. causal, understanding would allow us to predetermine the shape and properties of the function which will best describe the available data points. More data points allow a better and more detailed evaluation, revealing more aspects of functional relationships and thereby lead to increased understanding of the actual process involved.

Of course the classical rational method of hypothesis formulation and testing, leading to a mechanistic model, should be encouraged; however, it is recognized that useful application to real world problems will involve a considerable degree of integration of complicated process by means of simplified empirical transfer functions, i.e. simplified mathematical relations such as average values or linear equations.

A set of promising rational hypotheses are now available and these involve processes capable of exerting sufficient control on reproductive success such as to be discernible through the noise level of the multitude of additional processes. The following list is arranged in terms of physical processes, because both eggs and posthatch larvae are very much part of local physical processes, with the four categories containing results of recent research activity and interest and which are considered very promising avenues for further research.

(a) Vertical stability processes — Recent work (Lasker 1975; Hunter and Thomas 1974; IOC Workshop Report No. 28) has indicated a dependence of larval feeding success on fine-scale layers of food particles. These layers can be destroyed by vertical mixing (Kullenberg 1976; Owen 1981). Information on the structure, accumulation rate, nutritional suitability, and resistance to dissipation of such layers is required. The processes of sighting, approaching, attacking, and capturing appropriate prey organisms by larval fish take place on the microscale (millimetres to centimetres) and are believed to be strongly affected by turbidity and turbulence conditions. The interaction of water column stratification with turbulence generation is a key problem area. It is necessary to know how to formulate available wind data to indicate space–time windows sufficient for reproductive success (Bakun and Parrish 1981).

(b) Horizontal advection — Reproductive strategies often appear to be keyed to larval drift or passive transport mechanisms (Parrish et al. 1981). Larvae must be able to reach favorable nursery grounds. There appears to be a pattern of strong avoidance of offshore loss of reproductive products in the reproductive characteristics of stocks of coastal upwelling regions. Reproduction in areas of closed gyral circulation appears to be common. Where spawning is distributed in time and space or the larvae occur in the plankton over substantial time periods, very short-scale flow variations may tend to be integrated by the continuum of drifting larvae; thus a simple Ekman–geostrophic flow description may be adequate. Research on the use of established time series, such as sea level measurements or standard meteorological analyses, as indicators of flow variations should be encouraged. Variations in exchange of localized gyral circulations, which appear to be utilized in spawning strategies, within the larger-scale flow system should be investigated.

(c) Temperature — Rates of biological processes are controlled by temperature; extreme temperatures can be lethal. Thus temperature can usefully be used to define limits of occurrence. Anomalous temperature conditions, by changing growth or maturation rates, can cause disruptions and mismatches in time of critical life cycle events. A commonly cited example is the necessity for the production cycle of suitable food organisms to overlap with larval food requirements. In addition, temperature is a readily measured signal of important ocean processes (for example, in eastern boundary current regions, cool sea temperatures are often related to coastal upwelling and to horizontal advection from higher latitudes).

Temperature time series (depth profiled) which are characteristic of the space scale of reproduction are needed. Estimates of probable error are also required.

(d) Surface convergence or divergence — Horizontal structure (patchiness of larvae and their food organisms) is affected by convergence or divergence and associated frontal formation (Simpson and Hunter 1974; Owen 1981). Food availability and vulnerability to predation may increase in convergent fronts. Wind-driven Ekman divergence or convergence, which is controlled next to a coastal boundary by the alongshore wind stress and in the ocean interior by the wind stress curl, determine the vertical advection (upwelling or downwelling) in the upper ocean. Ekman suction and pumping can change slopes of ocean density structure and thereby alter current patterns. For example, in the California Current system the wind stress curl distributions coincide with the subpopulation structure of the major pelagic fish species (Parrish et al. 1981). This might also be the case in other areas.

Time series of ocean surface divergence processes and patterns should be developed and interpreted in a biologically relevant sense (Parrish and MacCall 1978). Error estimates are a particular requirement because a gradient of uncertain flow velocities is involved; errors are amplified in a derivative field of this sort. Horizontal mixing which would destroy spatial structure should be investigated. Linkage of frequency and intensity of frontal occurrence with large-scale surface convergence needs to be demonstrated.

The list could certainly be continued. For example, solar radiation is important to the production cycle as well as being a dominant stratification and turbulence energy source (i.e. winds). The biological interactions and their relationships with the physical variations should be studied. Any increase in rational understanding will allow better use of the very limited degrees of freedom in the available data.

Comparative studies appear a promising avenue for increases in understanding of processes that are difficult to address experimentally. For example, if there is a pattern of spawning by analogous stocks in semienclosed coastal gyres, one can reason that natural selection has operated to generate the pattern. Because natural selection implies reproductive success of preadapted individuals, it would be reasonable to assume that subsequent confinement of reproductive products within such a gyre is indicative of a significant survival factor. This provides a logical basis for development of a time series of variations in the strength of the gyre as an explanatory

variable to be included in an empirical model and from which the contribution of such phenomena might be evaluated.

Explanatory index series should probably always be tailored to the scale of the reproductive process involved, although minimum scale may be dictated by data availability. Where possible they should be associated with a data source that can be continued for a reasonable period and preferably be hindcast over past periods of fishery operation. Thus experiments and new types of technology will be most profitable where they can be used to 'calibrate' an existing time–series data source. Time scales of interest will correspond to spawning frequencies, although the controlling factor may be rather short-scale events; for example, in the case of the effect of wind mixing on larval anchovy first-feeding success, a relevant series would be the interyear variability of the occurrence of space–time 'windows' during which storm events above a certain threshhold intensity are absent (Lasker 1975; IOC Workshop Report No. 28, 1981, p. 15–104).

Stage II — Juveniles — Juveniles are here defined as young fishes, from metamorphosis to those stages where they live in the same place (time and space) as the adults and become available to fishing.

Little is known about this stage even in well-studied areas because: (a) there is a lack of good gear for sampling them; (b) they do not usually occur where the adults and the larvae occur.

It is at the juvenile stage that the 'fine tuning' of the recruitment numbers occurs. During this stage the fish actively move into the area occupied by the adults, where they must learn to survive or in which they must establish a territory, e.g. as in coral reefs. As compared to the situation in the larvae, where starvation or predation might be viewed as largely nonselective, predation on juvenile fishes may have a strong 'selective' component, with mainly unfit or smaller, slower growing fishes being removed from the system.

Juvenile growth is often seasonal (Brett 1979; Ricker 1979). Fish typically spawn prior to the onset of a "growth season." Thus, ambient temperatures and anomalies have a strong effect on juvenile growth and on the resulting length of time they stay in size-related predator fields, which are themselves temperature-dependent. Density-dependent growth is often evident at this stage.

Problem-solving for this stage will also follow a pattern of rational understanding of processes including testing and calibration against empirical data similar to that described for Stage I.

Example hypotheses of particular interest are:

a) that recruitment is limited by niche availability in the case of reef fishes;

b) for demersal fisheries an important hypothesis would be that predation by adult demersal fish is a strong and varying source of juvenile mortality which modulates recruitment;

c) for upwelling systems hypotheses about predation and mortalities related to advection need to be tested.

Research requirements would therefore differ among these various systems. A common problem, however, is the general lack of suitable gear for sampling this stage of the life history and development of suitable gear would seem urgent. The study of the ecology, distribution, movements, and interspecies interactions of juvenile fish (especially of commercial species) could help in closing a gap in our understanding of fish population dynamics, especially in establishing whether there are monitorable mechanisms which contribute to the suggested 'fine tuning' of recruit numbers, of which the order of magnitude will likely have been determined during Stage I.

Data requirements need to be closely related to the timing and scales of distribution of posttransformation small fish patches. These vary from metres to kilometres and have time scales of perhaps weeks to months. General ocean circulation patterns may be useful in developing an understanding of this life history stage. Distributions are in some cases localized and the causes of this need to be explained by examining features of the physical oceanography (fronts, gyres, etc.).

Stage III — Non-reproductive adults — Stage III is defined as the non-reproducing adults, including juveniles or maturing stages which have recruited into an exploited resource.

Although fishery biology is at its best when adult fishes are discussed, there are several areas where the OSLR Programme could help gain new insights, generate new hypotheses, and provide opportunities to test them. These relate to:

a) The spatial distribution of fish, i.e.:

i) with regard to fishes currently considered more or less limited to certain characteristic marine habitats (e.g. tuna species, or age-classes within species);

ii) with regard to the general rule that bigger (often, but not necessarily older) fish of a given species tend to occur in water deeper and/or cooler than the smaller (often younger) stages.

In both cases explanations have been provided which relate the temperature and depth of occurrence and/or water mass characteristics, including particularly oxygen content.

b) The natural mortality of fish. Natural mortality comprises both species-specific endogenous properties as well as exogenous causes, and both may be linked with environmental temperatures (and anomalies), and certainly with changes in the biological milieu.

c) Growth is strongly temperature-dependent, and both the zoogeography of fishes (occurrence of various species at various places — long-time scale) and the growth parameters at a certain time of a given stock (short-time scale) can be linked to changes in ambient temperature. Temperature would thus influence such things as population structure, size at first spawning, and fecundity and quality of gametes.

The OSLR Programme, by refocussing attention on the influence of long- and short-scale oceanographic phenomena on adult fish could help explain adult distribution, abundance and vulnerability to fishing gear (availability), and many growth-related phenomena (e.g. maturation, migration).

Stage IV — Maturing and spawning adults — Stage IV in the life cycle of fishes is defined by the onset of the reproductive cycle in the adults. On a population level this cycle can be seasonal or continuous. Recent observations, on *Engraulis mordax* for example (Hunter and Goldberg 1981), confirm the continuous population spawning (or batch spawning of individuals). The "fecundity" of such species thus becomes a concept that is difficult to evaluate. This single

parameter, fecundity, has often been used to calculate biomass of spawners from egg and larval survey data. It is important, therefore, to investigate more thoroughly the ability of populations to spawn continuously, and individuals repetitively.

There is little known regarding internal and external clues which initiate egg differentiation and maturation. Several effects appear to be related to temperature, among these differences in egg size and 'fecundity.' The thermal history of the juveniles and adults prior to Stage IV results in varying growth parameters and subsequently in varied fecundity, egg quality, and size. There are also apparent size–age effects on time of spawning and egg quality which are independent of temperature.

Little is known about how fish identify appropriate areas or locations for reproduction. There are several alternative strategies ranging from continuous sowing of gametes over the spawning season, to discrete, short-term spawning events (Sharp 1981).

Predation and Other Interactions Between Species

Species interaction is mainly caused by predation which here is interpreted in the most general sense, including man as the climax predator (Laevastu and Larkins 1981; Clepper 1979). Most management questions in some way relate to the concept of species interaction because it is only few stocks that, in practice, can be considered as isolated.

Our ability to predict short-term (1 yr) changes in stock composition to a large extent depends on our understanding of the mechanisms that govern predation on postrecruits. Possibilities of making probabilistic predictions of long-term (1–10 yr) changes in the stock compositions depend on our understanding of the predatory mechanisms as well as of recruitment.

Quantitative knowledge of predation mechanisms is still scarce, in particular, for the egg stage, the larval stage, and the juvenile stage. It is imperative, therefore, that as much information as possible on predation is extracted from available stomach content data. The few available stomach data sets can be used for making population level inferences in the sense that the stomachs from specimens of the same size sampled over broad areas and extended time represent predators that have been feeding in different geographic habitats. Data on the accessibility of various prey types during foraging is equally important as data on actual prey selection (stomach contents) to infer properties of the mechanisms governing food selection. Thus, stomach data sets, in particular for pelagic species, should be evaluated along with corresponding ecological data sets from the appropriate habitats. Approaches to bypass this problem are being developed based on Virtual Population Analysis or Cohort Analysis extended to account for species interaction (J. G. Pope, ICES CM 1979/H:16, ICES CM 1980/G: 19, unpublished data). There, total mortality for each entity of prey is partitioned into fishing mortality and natural predation mortality, and a 'residual' mortality (a coefficient accounting for mortalities due to causes other than predation).

Natural predation mortality is the fishery independent part of predation mortality, and is calculated by evaluation of an interlocking series of Virtual Population Analyses. This approach is necessarily based on various assumptions regarding the monthly or annual food consumption of each predator type (species, age, and size group) to reduce the number of unaccounted for variables.

Realistically, multispecies Virtual Population Analysis is a retrospective estimation of stock sizes that are in accordance with the observed stomach contents information. Evaluational classification of the relative importance of the various underlying assumptions is needed. For example, the derivation of reliable selectivity indices should probably not be done exclusively based on stomach data. This would require a prohibitive amount of stomach sampling. There is a need to combine the empirical approach with rational models of size selection (Beyer 1980). The only hypotheses presently available refer to size selection. One is the Andersen and Ursin (1977) log-normal selection model. There, it is assumed that a preferred prey size exists and that the ratio of predator size to preferred prey size remains the same throughout a predator's lifetime. This log-normal size-selection model is completely specified by two parameters — the relative measures of preferred prey size and selectivity broadness. No general hypotheses seem to be available with respect to interspecific differences in vulnerability to predation. Differences in vulnerability or desirability may be caused by differences in the external protective structures and avoidance behavior of the potential prey types.

Rational models will help in identifying data requirements and designing experiments on various scales to improve understanding of species interaction as well as help in utilizing the already available information on predation.

The complete story of predation is about why most fish die and why some of them survive. Predation is simply a sequence of perceptions, decisions, and actions of predators about their prey. This is, however, oversimplified. Apparently predators often encounter prey organisms one at a time. Their feeding strategy and success depends on several factors including their state of hunger, experience or skill level, adaptation to certain prey types, and probably many other factors apart from their size or species. Filter feeders depend on similar recognition and reaction to their prey, depending on their hunger state and other stimuli.

The degree to which it will prove necessary to distinguish between different predators — sometimes considered as identical — and to incorporate knowledge of their various feeding strategies depends on the marine ecosystem in question and the nature of the problem to be addressed. At present, however, it is not even clear what the basic differences in feeding strategies are that allow closely related species to coexist. In the first instance, there is a need for observations of individual feeding behavior. This type of process-oriented data collections must to a large extent be carried out *in situ* for juvenile and adult fish. Additional studies in tanks or enclosures of sufficient size to avoid behavioral or activity constraints may help in clarifying concepts. Other fields which clearly require more experimental studies are digestion and gastric evacuation. Basic principles of the digestive process are not yet understood and this limits understanding of the relationship between stomach contents and actual food consumption.

The possibilities of evaluating causal aspects of vulner-

ability to predation by comparing characteristics (e.g. condition or parasite burden) of freshly caught prey found in the stomach with live prey of the same characteristics, i.e. specimens of the same length, could prove important.

In the early life history stages experimental studies may be of considerable help in identifying feeding mechanisms, requirements, and limitations for growth and survival. These studies would be most informative if performed in simulated mini-ecosystems (or laboratory microcosms). This, among other things, requires the ability to measure and perhaps control the species, size, and spatial distribution of plankton. Nearly all experimental studies with larval fish have been carried out at food densities in great excess of what is usually found by integrative measurements taken in the sea via nets, pumps, or other techniques. Intensive studies of growth and survival of larval fish, with and without larval predators, with interpatch zooplankton densities in the order of 10 plankton per litre are needed. To be useful such studies need to be carried out so that there is enough data collected to permit alternative, statistically testable hypotheses on growth and survival to be resolved. This is not possible with current measuring techniques. Techniques are needed for precise and automatic detection and monitoring of local (centimetre to metre scale) densities and sizes of plankton (10 μm−3 mm) and fish larvae (3 mm−30 mm) without disturbing the system. The usefulness of optical or acoustic techniques for this purpose — for application both in the laboratory as well as in the field — needs further investigation.

Major Systems of Interest

Systematic ordering of the stages in the life cycles of fishes leads directly to scaling problems and to questions of appropriate research methodologies which might be used to study these different stages and scales. There are other important considerations which are also very restrictive in the sense of scaling and approach, namely biogeographic or ecosystem considerations. In the higher latitudes, which have been purposefully deleted from detailed discussions, seasonality of production is the dominant variable, with a resultant selection in evolutionary contexts for annual cycles and longevity in the dominant fish species. In the tropical and subtropical regions a full spectrum from seasonal to nearly continuous production patterns are observed. Also, much of the biomass comprises large numbers of small, short-lived, rapidly responding species (Pauly 1979), whereas the larger, longer-lived species, although present, tend to be of relatively low abundance in most systems, because of their relatively high position in trophic webs.

In an attempt to focus attention on systems likely to be important to developing countries, four basic regimes were selected as representative of characteristic habitats. Certainly there are distinct differences among the several manifestations of these types or systems, but because of overriding physical biological effects, similarities have emerged which make generalization within each type of system possible.

Upwelling Systems

The upwelling regions of the world are characterized by high productivity and massive pelagic fish stocks which exhibit extreme fluctuations. Recent research indicates that coastal upwelling can be driven both by local wind forcing and by disturbances propagating from elsewhere. On experimental time scales (fractions of a day to several weeks), propagated effects seem to contribute relatively greater variance in tropical systems than in subtropical or temperate systems. Thus the collapse of the California sardine stock has occurred in a system that appears to be predominantly locally wind-driven. Collapses of the anchoveta in the Peru Current, and the sardinella in the Guinea Current, have occurred where at least the shorter-term fluctuations are uncorrelated with local wind variations.

The upwelling system off southwest India appears to be an extreme case of noncorrespondence to local wind forcing. Here the upwelling season coincides with the southwest monsoon, when the prevailing wind tends to be directly toward the coast. Thus the offshore surface Ekman transport which would drive locally produced upwelling actually vanishes at the very season when upwelling is most evident. Possible explanations include coastal trapped wave propagation around the southern tip of India from an area of offshore-directed surface transport on the east coast. It is also possible that the Somali Current circulation, which leads to a southwest current off southwest India during the southwest monsoon, may be contributing to the observed upwelling through interactions with bottom topography (onshore-directed bottom Ekman layer, etc.). The stock of oil sardine off southwest India has been subject to extremely wide long-period variations, appearing in such large numbers during the upwelling season as to constitute the major single-species fishery resource during certain groups of years, while being virtually absent over other multiyear periods.

The particular massiveness of the fish stocks inhabiting upwelling regions suggests that upwelling is a basic mechanism in maintaining them. Most of the recently developed understanding of the dynamics of upwelling systems concerns the shorter time scales which are most readily addressed by experiments. However, the observed stock variations occur on long (seasonal and interyear) time scales. Even off Peru, the Coastal Upwelling Ecosystem Analysis (CUEA) studies suggest that the quasisteady upwelling which may underly the energetic shorter scale fluctuations may actually be locally wind-driven. Understanding longer term variations in the upwelling system could lead to insights into the interacting effects of exploitation and environment on stock variations which would yield improvements in the management and exploitation of these resources.

Coral Reefs

Coral reefs contribute significantly to the world's total fishery catch. Yet the overwhelming part of coral reef research is ecologically oriented and conducted predominantly by marine biologists, ecologists, and ethologists, with very little input going into applied questions relevant to fishery biology and resource management.

Among the more urgent questions pertaining to the exploitability and long-term productivity of coral reefs are those relating to the recruitment of young fish to the coral reef

populations. In this context, emphasis should be given to the separation of reef systems which produce their own recruits from those which receive their recruits from neighboring reef systems, and to the transport mechanisms by means of which recruit transfers take place. Answers to these questions, which could help in the identification of suitable areas for underwater national parks or broodstock reserves, would be of considerable interest to countries whose reef resources need protection. An interesting question for fishery science would be an assessment of the range of influence of such reserves.

The study of the interactions between coral reef fishes could also help in elucidating the process of predation and its possible role in stabilizing and structuring reef populations. The study of fish predation in reefs would also help to answer questions pertaining to energy transfer between trophic levels and to the role of large predators in relation to a fishery.

Likely areas in which to conduct such research are the Caribbean, where previous research has laid a solid groundwork to start from, and the Great Barrier Reef, where the replication of experiments would seem easiest.

Tropical and Shelf Demersal Fisheries

Catches from tropical shelf demersal fisheries are characterized by large numbers of species. There is great difficulty in obtaining fisheries data at the species level. In some areas research surveys have provided useful time series of abundance changes by species groups and these suggest a greater stability with respect to the environment than temperate systems exhibit. This may, however, be simply an impression created by ignorance of such factors as recruitment or catch of each species, or even due to the behavior of the fishermen themselves.

The development of fisheries research in these areas will probably be dominated by surplus production models for some time in the absence of data for more analytical approaches. An approach to analytical techniques may be made by estimating growth, mortality rates, and recruitment for certain representative species. Until this is done, it may be premature to initiate major programs aimed at understanding the biology of, for example, the early stages of the life history.

More pressing scientific problems would seem to be a comparative study of the factors that effect productivity (primarily of fish) in these areas. A comparative study might, for instance, be carried out in the South China Sea area with the aim of explaining abundance or yield in terms of environmental features. Because the demersal fisheries there seem to operate in semiestuarine systems, it seems probable that runoff may be a key factor. Such a study might enable surplus production modeling applications to be generalized over this area and might also enable species successions resulting from fishing pressure to be predicted. The time scale of such an investigation might be by month and the size scale by about 50-nautical-mile lengths of coast. These scales would doubtless need to be adapted to fit with topographical details.

Results from the Gulf of Thailand, Indonesia, and elsewhere suggest that fish stocks in the area may be rather localized. Various groundfish surveys indicate different trends in abundance in different areas. If the fisheries in such areas are based on various small substocks this will have important implications for the management of these fisheries. Scientific studies of stock divisions in such areas may therefore be of value. Tagging/meristic/genetic studies would seem indicated in the first place but studies of ocean circulation processes and larval transport may be indicated to back these up. The size scale of these studies might be of the order of 100–200 nautical miles of coastline.

Certainly given the contribution of mangrove and other brackish-water systems to coastal fisheries, a tremendous research effort is required to evaluate the dynamics and dependencies in these complex ecosystems which affect subsequent production. Here again, scale will be of great importance.

Oceanic Pelagic Fisheries

The oceanic environment is perplexing in that there are many broad provinces with physical–chemical–climatic properties which can be labeled, but the occurrence of resource is patchy within these provinces. The major apparent abundances and vulnerability zones of the resources are often at interfaces of the physical–chemical provinces, including the thermocline. There are examples of unconventional resources which have recently come to our attention (e.g. Antarctic krill, mesopelagics off Oman).

There are undoubtedly others. With ever-increasing insights arising from marine exploration (for example, recent location of deep-water thermal and freshwater vents), new potentially interesting sources of productivity are being identified, and in some cases commercial species are found associated with them. Often only the knowledge of the sources of the productivity helps to dispel some of the uncertainties in fishery resource contexts.

Important questions still exist about the transfer of energy in deep ocean systems to the larger, but not particularly numerous apex predators.

Tunas and their kin (the genera *Thunnus, Euthynnus, Katsuwonus, Auxis*) are special cases requiring specific modes of study. However, considering that they are presently under investigation by large bodies with diversified interests, other open ocean resources can be identified which should perhaps receive more attention. At least three — rainbow runner (*Elagatis bipinnulata*), dolphins (*Coryphaena* spp.), and oceanic sharks — seem to be of sufficiently greater potential commercial interest than presently exhibited that they certainly warrant further attention in this context.

The deployment and monitoring of open ocean-aggregation devices for the explicit purpose of concentrating relatively diffuse, but not particularly abundant individuals or small schools of oceanic predators (including the species mentioned above) could provide both scientific insight into aggregation cues and improved utilization of these resources. In a broader context, studies of these predators' behavior and ecological properties could also help in determining their impact on pelagic and coastal ecosystems.

Suggested Studies

Two approaches to fishery/environment studies are possi-

ble — detailed studies of particular situations (e.g. anchovy in the California current), and comparative studies of similar systems (e.g. coral reefs). The latter has two aspects. There is the direct practical aspect in which a fishery scientist working in a poorly studied area can obtain some insight into how his or her questions might be answered (and possibly also some of the answers) by analogy with a better-studied area. The other is of more general scientific interest and results from examination of data from a number of similar systems (no one of which may have been studied in depth) to identify patterns and differences and thus obtain insights into how each system operates.

These approaches are all valuable, but it is important that a proper balance is maintained. In particular the Group felt that it was vital to have high quality in-depth studies of at least some representative examples of each of the main systems discussed in this report. Such studies cannot be done for all examples in each system and some selection must be made. In the context of OSLR it is fortunate that there are examples of most systems of interest to developing countries off the coast of, or close to, developed countries with high-quality expertize in the marine sciences (eastern boundary currents off California and Portugal/northwest Africa; coral reefs off northeast Australia; tropical shelves in the Gulf of Carpentaria and the Gulf of Mexico). Many of the necessary detailed studies might well be conveniently carried out in these areas. Participation by scientists from developing countries in these studies should be encouraged and facilitated, e.g. through cooperative research programs and fellowships, though this should not rule out the execution of detailed studies off developing countries where sufficient expertize can be brought to bear. At the same time assistance should be given to developing countries with respect to their own systems, especially in the compilation and analysis of data that might be used in comparative studies, and in the identification, formulation, and pursuit of relevant research topics.

Access to Data

The participants noted the instructions to the IOC Secretary (IOC Resolution XI-17 to "... develop through correspondence an inventory of information ..." on subjects of marine ecosystems.

Dissemination of data and information is not a new problem, but the multidisciplinary studies that will be required in OSLR add a new dimension to the problem. Not only must, for example, data on physical oceanography be available to fishery scientists, but they should be available in a form that the fishery scientist can readily interpret and employ by combining it with fishery data to study the effects of varying environment on fisheries. The same is true as regards the possible use of fishery data by oceanographers and others.

Many of the basic environmental data (e.g., sea surface temperatures) can be located through the World Data Center System, the IOC Marine Environmental Data Inventory (MEDI), and both national and regional oceanographic data centers; marine meteorological and climatological data can be obtained through the World Data Center System and the World Meteorological Organization (WMO).

The products of these data centers are often not in the form that a fishery scientist can conveniently use, even when the figures presented are the ones of interest. There is a need for presentation of the relevant oceanographic data in a form and on a time and area scale that are directly applicable to fisheries. It might be a later task of OSLR to identify more closely what the relevant data and the appropriate time and area scales are, as well as to identify the locations where such data would be most useful. In addition to the basic data stored in the Data Centers there are quantities (e.g. wind stress curl) that can be derived from these — and may be directly relevant fo fisheries, but which are not generally available. These need to be calculated, and an appropriate format will be required for each study program depending upon time−area scales of interest.

The problems of making fishery data available to non-fishery scientists are even more difficult. Basic fishery statistics (particularly of fishing effort and corresponding catch) are the most widely used source of data in monitoring the abundance of fish stocks. However, the interpretation of the types of data generally available is full of potential pitfalls (much of the work of fishery scientists is concerned with the suitable adjustment and interpretation of this type of data) so that they are not generally suitable for direct incorporation in data centers, to be used by the unwary without further guidance. Nevertheless, there is a large volume of fisheries data which could be most useful to environmental scientists if they were aware of them and could be guided in their use and interpretation by someone familiar with the fishery concerned. It was therefore suggested that it would be useful if a catalogue or inventory of such data could be developed (perhaps by FAO), setting out for each country and fishery for which data series exist: the nature of the fishery (major species and methods of fishing), the period over which data exist; the nature of the data (e.g. units of fishing effort used); the form in which the data are recorded (e.g. annual statistical reports, unpublished notes, files on magnetic tape); and the institution to which enquiries should be addressed.

Concluding Remarks

Regional or fishery scale multidisciplinary scientific fora for the exchange of information, formulation of projects, and coordination of activities will be of primary importance to the success of the OSLR programs. Equally important will be the individual and institutional efforts necessary to disseminate and apply existing knowledge and techniques for resolving questions relevant to living resources. These efforts need no further justification; what is needed is dialogue and action.

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Comment on "Short-term Forecasting in Marine Fish Stocks"

COMMENT

In a recent paper Stocker and Hilborn (Can. J. Fish. Aquat. Sci. 38: 1247–1254) demonstrate that the methods of my 1961 paper give forecasts of future catches that are less reliable than most other methods. I would have been somewhat disappointed at this, though not altogether surprised after 20 yr, if in fact my paper had dealt with forecasting. Using the notation of Stocker and Hilborn, the two relevant equations in my paper can be written as

$$(1) \quad U_t = a + b\,\overline{E}_t$$

and

$$(2) \quad C = AE + bE^2$$

where equation (1) describes the catch per unit effort in year t as a function of the average effort over the previous K yr i.e. $\overline{E}_t = \frac{1}{K}(E_t + E_{t-1} + \ldots E_{t-K} + 1)$ and K is the average life expectancy of a fish in the fishery. Equation (2) describes the relation between catch and effort in the steady state. Here it might be stressed that as my method was described the potential life span of an individual fishery would be much larger than K; for the Iceland cod that were recruited at around 3-4 yr old and could live to 12 yr or older, then a value of $K = 3$ was used. However, it seems that in later applications a value of K equal to the potential life span has been used. This would seem to give undue weight to the effort some years in the past.

The above equations were as close as my original paper came to making forecasts. However, Stocker and Hilborn (their equation 2) modified them to forecast the catch in year $t + 1$, — assuming the effort E_{t+1}, and the effort in previous years are known — using the equation

$$\hat{C}_{t+1} = a\,\overline{E}_{t+1} + b\,\overline{E}^2_{t+1}.$$

From this the corresponding prediction for the catch per unit effort can be deduced as

$$\hat{V}'_{t+1} = (a + b\,\overline{E}_{t+1}) \times (\overline{E}_{t+1}/E_{t+1}).$$

This differs from the value of the catch per unit effort which would be predicted directly from the model by the factor $(\overline{E}_{t+1}/E_{t+1})$.

If I were now to adapt my 1961 model to predicting future catches, I believe the most reliable way would be to predict the CPUE from the model, and deduce the catch from that prediction, and the effort, i.e. to use the prediction

$$\hat{V}'_{t+1} = a + b\,\overline{E}_{t+1}$$

$$\hat{C}'_{t+1} = (a + b\,\overline{E}_{t+1})\,E_{t+1}.$$

As I do not have access to all the original data used by Stocker and Hilborn, I have not been able to check whether the above, theoretically more attractive, equations do in fact give better forecasts, though it does seem that they would avoid some of the main discrepancies between forecast and actuality. For example, Table 1 of their paper shows that in 1973 the so-called Gulland method grossly overestimated the catch. This error seems in large part to be due to the actual effort, E_{t+1}, being much less than $\overline{E}_{t+1}$, though as it is not clear what value of K has been used, this cannot be checked directly. It would be interesting to see the results of recalculating Stocker and Hilborn's analysis using the above equations (as well as the similar adjustment to their equation (71) for the Fox formula).

Having attempted to defend the value of my version of the production model, suitably interpreted, for prediction, I would also stress the value of the two general points raised by Stocker and Hilborn — the potential importance of looking at the predictive ability of commonly used models, and the difference between the ability of a model to predict next year's catch, and its value as a tool for management. That the ability to predict is the real test of a scientific theory is commonplace in discussing the methodology of science, but in this context prediction is not so much a matter of forecasting the next point in a time-series, as of predicting the effect of changes in one or other factor of specific interest (e.g. the fishing effort) on the other characteristics of the fish stock and the fishery — J. A. GULLAND, *Chief, Marine Resources Service, Fishery Resources and Environment Division, Food and Agriculture Organization of the United Nations (FAO), Via delle Terme di Caracalla, 00100 Rome, Italy.*

REPLY

Gulland is correct in pointing out the problem in using averaged efforts to forecast future catches in our recent paper. Using Gulland's alternative forecasting equation, the performance of his method is improved. In several cases, the improvement is dramatic; for the Middle Hecate Strait rock sole and Hecate Strait English sole stocks, Gulland's method explains 60% of the variation in catches (our statistics $1 - D/\sigma^2 = 0.6$). For the English sole stock, Gulland's method is the best forecasting method. In overall performance on the five stocks we used, the changed equation improves performance from fifth out of seven to fourth out of seven.

For readers interested in repeating our calculations, the K values we used were 5 for the two rock sole stocks and the Eastern Pacific yellowfin tuna, 4 yr for Hecate Strait English sole, and 3 yr for the California sardine.

Our revised analysis suggests that Gulland's method may be as suitable a forecasting tool as any of the other methods we tested. However, as noted in our paper, and in Gulland's comment, the 1-yr-ahead forecasting ability we tested does not test the utility of a method for long-term management.

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Management utility of methods could in principle be tested by seeing how well the methods would predict into the future (perhaps 10 yr) given future efforts. Thus we would ask if each method would have predicted the collapse of the California sardine given the future efforts. To our knowledge, this has not been done, although D. Roff (Department of Biology, McGill University) has tried 1-, 2-, and 3-yr-ahead forecasts. We suspect that such tests would be most useful where either catch or effort underwent a dramatic change. It is certainly an interesting area for further work. — MAX STOCKER, *Department of Fisheries and Oceans, Resource Services Branch, Nanaimo, B.C.* AND RAY HILBORN, *Institute of Animal Resource Ecology, University of British Columbia, Vancouver, B.C.*

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BOOK REVIEWS/COMPTES RENDUS

Fisheries Oceanography and Ecology, *Taivo Laevastu and Murray L. Hayes. Fishing News Books Ltd., U.K. 1981. 216 p., 81 illus. £ 19.50.*

This book is the third revised edition of *Fisheries Hydrography* by Laevastu and Hela, 1962. I purchased the first edition and was reasonably pleased with its content; there is no need for me to purchase the 1981 edition because little has changed except the cover and the authors. Less than 20% out of 300 references are from publications dated later than 1970. During a period in the history of fisheries science which has seen the collapse of much traditional theory, the authors put forward a modest one sentence (p. 25), "The year-class strengths in most fishes are determined by factors other than the size of spawning stock," to be followed, not by a discussion of recent information on the survival of early life stages, but instead by an almost religious discussion of the effects of temperature on spawning and egg development (8 p.), the effect of temperature on fish distribution (11 p.), the effect of temperature on catching fish (6 p.), and the effect of temperature on sound (5 p.).

On p. 25 the authors state "The survival of larvae is dependent on the availability of proper planktonic food at the right time and place," but nowhere is there a discussion of the match and mismatch theory of Cushing (e.g. Cushing 1975) or of Lasker's work on anchovy survival (e.g. Lasker 1975) to cite two of many omissions on this subject. A refreshing quotation from Hempel (1978) p. 51, regarding changes in the North Sea fisheries, is reproduced without any discussion of previous or subsequent ideas regarding the North Sea ecosystem. A statement on p. 52 says that "Good, comprehensive fish food studies are very few indeed," and is followed on the same page, three lines later, by "A voluminous amount of literature is available on the food and feeding habits of fish." In fact, the book deals with neither the "voluminous literature" nor the "good comprehensive studies" that are available.

Illustrations and layout of the text are improvements over previous editions. Some new sections on ocean analysis and numerical ecosystem simulations represent steps in the right direction towards fulfilling the purpose of this text on how oceanographic data can be used to benefit fisheries. However, even in these new sections the authors do not avail themselves of the literature available, but instead represent the views of the authors (e.g. the last chapter on ecosystem simulations is only referenced by a single paper attributed to the senior author). A number of sections contain purely factual information in terse statements, for example, on p. 82 there are six paragraphs in half a page, each of one or two sentences, which state findings of six authors with no interpretation or evaluation such as one would expect in a text.

In summary the book appears to be a highly personalized view of the state of Fisheries Oceanography and Ecology and not a textual review of the subject.

CUSHING, D. H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge, U.K. p. 181.

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Aquatic Toxicology. *Elsevier/North-Holland Inc. Bimonthly. $92.25 U.S. (ca. $100 Can.) per volume.*

Fisheries Research. *Elsevier/North-Holland Inc. Quarterly. $59.25 U.S. (ca. $70 Can.).*

North American Journal of Fisheries Management. *American Fisheries Society, Bethesda, MD. Quarterly. $10 U.S. (or equivalent in Canadian funds). Libraries $70 including other American Fisheries Society journals.*

Journal of Crustacean Biology. *The Crustacean Society, Washington, DC. Quarterly. $25 U.S. in North America, $30 elsewhere.*

There are those who automatically decry the publication of a new journal on the basis of the proliferation of scientific publication, but this tendency must have been identifiable ever since the fine old days when the Fellows of prestigious Academies and Royal Societies could comprehend each others' presentations at small discrete gatherings. The test of a new publication will surely be the authors it attracts, the circulation it creates, and the quality of work accepted. The latter test is perhaps best made in retrospect, particularly as fads have been known to cause rejection of truly original and therefore contentious contributions from highly reputable journals, while allowing space for the gracefully executed traditional study. Judging journals by their first issue is particularly difficult in this regard as wise editors will solicit a sufficiently worthy set of initial papers with which to launch their latest venture. The objectives of the journal may be more useful than the content alone, and here we have two contrasting sources and motivations. The two Elsevier journals contrast with the others in not being sponsored by scientific societies, the traditional parents for journals. *Aquatic Toxicology* provides a useful outlet for a rapidly expanding discipline, and has good geographic balance between Europe and North America. Though in taxonomic terms the emphasis is completely on fish, this is modified in later issues. The focus here is fairly tight, whereas that of *Fisheries Research* is not. Whereas the best fisheries laboratories combine gear research, administration, practice and theory, economics, policy, science, and naval architecture, I do not see too many staff members at such institutions reading each others' contributions to such a broadly based journal. The geographic coverage of authorship here is broad, the emphasis is on gear

and technology apart from one paper on the Alaskan fur seals.

The American Fisheries Society has launched its companion to the Transactions with an appeal to its own membership for support, and its policy statement refers to a target audience of fisheries managers (who are permitted to retain their non-metric tradition by allowing units to be cited in either metric or English, but not both — a confusing policy and surely a missed opportunity). The breadth of coverage, though, leaves me wondering if the preponderance of freshwater problems will be of interest to the same audience as work on marine fisheries being actively solicited, and the environmental study on dredges might be better placed elsewhere.

Whereas all three journals already discussed focus on the growing volume of applied science being executed in the current political climate, the Crustacean Society provides one of the few new outlets for unashamedly basic work upon which the applied studies must of necessity be based. A great deal of basic taxonomy and phylogeny is presented, work that other journals often cease to accept under pressure of physiological, ecological, and applied work, but again, adherence to a firmer policy might suggest that stream drift of macroinvertebrates would be better reported elsewhere.

The difficulty with any journal accepting work from a wide variety of disciplines is that the editors cannot hope to include the best possible reviewers for all the material they receive. Nothing is more annoying than to see published work that would have been greatly improved by review by any one of a handful of specialists, but which contains errors, duplications, and oversights despite the peer review method.

Selection of journals as reader or author will inevitably be personal and not even necessarily objective. My preference is for journals with a narrow focus and high reviewing standards which allow me to minimize the number of periodicals to be scanned. If I have any hope of retaining the classical scholarly breadth of interest, I can achieve this by scanning several specialist journals. My shelves are no longer burdened by the long series of publications which contain one paper of interest a year — the abstracting services have rendered them inefficient in their prime objective, the dissemination of accurate new information and ideas.

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COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

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Patterns of nitrogen excretion and oxygen consumption during ontogenesis of carp (*Cyprinus carpio*) **S. J. Kaushik, K. Dabrowski, and P. Luquet**

Planktonic ciliates: their distribution, abundance, and relationship to microbial resources in a monomictic lake **M. L. Pace**

Aspects of larval lobster (*Homarus americanus*) ecology in St. Georges Bay, Nova Scotia **G. C. Harding, W. P. Vass, and K. F. Drinkwater**

Horizontal exchange on central Georges Bank **J. W. Loder, D. G. Wright, C. Garrett, and B. A. Juszko**

Fixation shrinkage of herring larvae: effects of salinity, formalin concentration, and other factors **D. E. Hay**

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